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BY

DENNIS G. RAINEY

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EASTERN WOODRAT, NEOTOMA FLORIDANA: LIFE HISTORY AND ECOLOGY

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CONTENTS

Introduction

The objectives of the study here reported on were: (1) to ascertain the range of habitat occupied by the eastern woodrat, *Neotoma floridana* (Ord), in eastern Kansas; (2) to study the life history of the species by means of a long term live-trapping program; (3) to determine those factors in the environment which affect survival, and (4) to attempt to discover factors limiting dispersal and occupation of new habitats. My study was done mostly in the field but laboratory investigations were an integral part of it.

Live-trapping was initiated in March, 1951, and terminated in June, 1954. A part of the area chosen for live-trapping is on the University of Kansas Natural History Reservation and the remainder on adjacent privately owned land. The Reservation is a tract of 590 acres set aside in 1948 as a natural area for the preservation and study of plants and animals native to Kansas.

Woodrats were studied taxonomically and results made available in the excellent report by Goldman (1910). Even though many more forms of woodrats have since been discovered and described and distributions more accurately ascertained, a thoroughgoing revisionary study has not been made since that of Goldman, and one is much-needed. Detailed accounts of life histories have been set forth for *N. fuscipes* by Linsdale and Tevis (1951) and for *N. albigula* by Vorhies and Taylor (1940), but little has been published concerning several of the widespread species such as *N. lepida, N. mexicana,* and *N. micropus.* The study by Finley (MS) adds much to knowledge of the ecology of these lesser known species. Species restricted to Mexico are even less known. Numerous reports of somewhat lesser scope dealing with certain phases of life history have been published for other species such as that of Poole (1940) on *N. magister.* Scattered information for most of the species but concerned principally with habitat is to be found in the numerous faunal reports. A thorough study of the life history and ecology of the eastern woodrat has not been made heretofore. Excellent reports by Hamilton (1953), Murphy (1952), and Pearson (1952), are limited in scope. All available literature has been investigated and used in this report whenever pertinent to the discussion.

Woodrats are not commonly seen because of their nocturnal habits, but they are not unfamiliar to the general public. Many stories are told concerning the "trading" propensities of woodrats, or pack rats as they are frequently called. Woodrats are not averse to living in barns, and when they do, they often are confused with

the non-native murine rats. The hairy tail, large hairy ears, large eyes, and soft pelage serve to distinguish woodrats from the introduced Old World species of rats.

Woodrats are not of great importance economically in the United States although they are utilized as food in parts of Mexico.

Several persons have been of great assistance throughout the period of study and without their aid this report would have been difficult to complete. Dr. Henry S. Fitch, Resident Investigator of the Reservation, has devoted many arduous hours to counseling, assisting with field problems, and aiding in preparation of this manuscript. His unselfish help is acknowledged with sincerest gratitude. I am grateful to Professor E. Raymond Hall for his encouragement and assistance in critically reading this manuscript and to Professors A. B. Leonard and Rollin H. Baker for valuable suggestions and advice. I would like to express special thanks to the following for identifying ectoparasites: Dr. Richard B. Loomis of Long Beach State College Department of Zoology for identifying the chiggers; Mr. Earle Cross of the University of Kansas Department of Entomology for identifying the fleas; Dr. Curtis Sabrosky of the United States National Museum for identifying the cuterebrid parasite; and Dr. Glen M. Kohls of the Rocky Mountain Laboratory for examining the ticks. I am indebted to all my friends and associates who have aided in various ways and finally, to my wife, Bettye Rainey, for assistance with field work and preparation of this manuscript. All photographs were made by the author.

Methods

The live-traps used, patterned after those described by Fitch (1950:364-365), were of one-half inch hardware cloth, five inches high, five inches wide, and 20 inches long. Wooden nest boxes were constructed so that they would fit into the rear of the traps which were left open for this purpose. The boxes were soaked with linseed oil and painted on the outside to waterproof them. The inside dimensions of the box were just large enough to accommodate an adult rat. Several traps with large vegetable tins attached to the rear for nest boxes were used later in the field work, but these were not so satisfactory as the former because often they could not be inserted under rock ledges. A few traps without nest boxes were used. They were as efficient as those with nest boxes if placed under a protective ledge of rock (Plate 1). Large wooden rabbit-traps with an outside string as a part of the trigger

mechanism proved inefficient because woodrats persisted in removing the string.

In winter, each trap was supplied with enough cotton so that a warm nest could be fashioned by a captive woodrat. The nest box was not large enough to permit making the nest inside, but the captive would pull out the cotton and form the nest on the floor of the trap (Plate 1). A gallon-sized anti-freeze can cut and shaped to form a hood covering the wire part of the trap was effective in preventing rain or snow from reaching the cotton nest (Plate 1). In summer pieces of board wider than the trap were placed on top to provide shade when necessary. Pieces of screen wire were fastened over the bottoms and the sides of the traps posterior to the triggering mechanism to prevent losing bait. Before screen was used, white-footed mice, *Peromyscus leucopus* (Rafinesque), would undermine the trap and remove the bait which had fallen through.

Several kinds of baits were tested. Mixed grain ("chick scratch"), combined with raisins proved to be the bait most consistently acceptable, and most economical. Either meat or raisins alone would attract woodrats, but in summer these baits were unsuccessful because of interference by ants. When mixed with "chick scratch,"

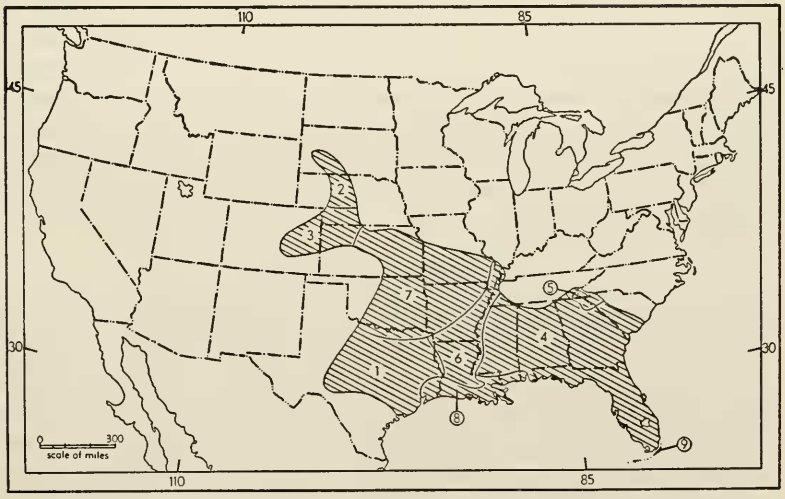


FIGURE 1. Geographic distribution of *Neotoma floridana*.

1. *N. f. attwateri.*
2. *N. f. baileyi.*
3. *N. f. campestris.*
4. *N. f. floridana.*
5. *N. f. haematoreia.*
6. *N. f. illinoiensis.*
7. *N. f. osagensis.*
8. *N. f. rubida.*
9. *N. f. smalli.*

raisins rapidly lost most of their moisture and were then less attractive to ants. A quantity of chick scratch with a few raisins to attract the rat was placed behind the trigger or directly in the nest box. A small amount was scattered in front of the trap.

Live-traps were not placed according to a prescribed pattern. One or more traps were placed at each house and, when trapping at a rock outcrop, I placed additional traps at sites where sign, such as accumulations of droppings, were present. If a trap failed to yield a capture after several nights, it was usually moved. Large rocks were used to anchor the traps to minimize disturbance by predators. The doors of the traps were rigged so that they would lock after being sprung, and some traps were wired firmly to large rocks or to adjacent small trees. However, on many occasions, predators succeeded in opening traps.

Description

General

Like most other members of the genus, this species in external appearance is characterized by large, rounded, and sparsely haired ears; tail covered with short hairs; large black eyes; and soft pelage. The large eyes, which protrude from the head, are characteristic of an animal nocturnal in habits. The toes, four on the front feet and five on the rear feet, have well-developed sharp, downwardly curved claws. Large apical and palmar pads aid in climbing. The vibrissae may extend to a maximum distance of 75 millimeters on either side of the nose. The muzzle is pointed but there is no obvious demarcation between it and the forehead. The body is compact, robust, and highly muscular in large males. The skin is thickened in older individuals of both sexes.

External Measurements

External measurements, in millimeters, of 48 adult specimens, 28 males and 20 females, in the University of Kansas Museum of Natural History indicate that males tend to average slightly larger in total length, length of tail, and length of hind foot. Measurements (total length, length of tail, hind foot, and ear) for 28 males are: 374 (305-450), 160 (130-180), 40 (35-49), and 26 (23-30). Measurements for 20 females are: 369 (300-399), 157 (130-172), 39 (35-42), and 26 (24-29). These specimens, all of the subspecies *osagensis*, were collected in Douglas, Marshall, Ellsworth, Anderson, Greenwood, Jackson, Jefferson, Chase, and Cowley counties, Kansas.

Weights

Males attain greater weights than females. The largest weight recorded for a male on the study area was 384 grams; the next largest weight was 375 grams. Females because of pregnancy and nursing young vary more in weight over periods of time than do males, but the males also fluctuate. Sometimes they suddenly lose weight; for example, an adult male that weighed 365 grams on April 22, 1951, had declined to 290 grams eight days later. Three days later his weight had further declined to only 260 grams, representing a net loss of 105 grams over an eleven-day period. After one month, his weight had increased to 375 grams. In general, adult males tend to reach their peak in weight in February and March at the beginning of breeding season, and decline to their annual low point in May. There is a fairly rapid recovery of the males in June, when most females are having litters. There are other slight declines in July, probably because of extreme hot weather, and in September and October as activity in storing of food increases. In late autumn and winter, weight steadily increases until the peak is again reached.

The average weight of 21 adult males when live-trapped the first time was 299 grams (220-384). The average weight of 23 subadult males when live-trapped the first time was 197.4 grams (130-250). The average weight of 14 non-pregnant adult females was 216 grams (174-260).

Color

The dorsal surface varies from Sayal Brown (capitalized color terms after Ridgway, Color Standards and Color Nomenclature, Washington, D. C., 1912) to Snuff Brown, tinged with black in varying intensities. The black wash is more intense on the back than on the sides and tends to be slightly darker in winter than in summer at which time it varies from Sayal Brown to Clay Color. The dorsal surface in worn summer pelage preceding molt becomes bright Orange-Cinnamon. A lateral line of Pinkish Cinnamon, usually obvious in winter pelage, is indistinct in summer pelage. In winter this color extends over the front legs and under the armpits on the chest but not to the mid-ventral line, and it covers a larger area on the chest in winter than it does in summer. The head is generally the same color as the dorsal surface but becomes grizzled in older animals.

The ventral surface is whitish. Hairs in the pectoral and inguinal regions are usually white to the base; hairs on the sides of the abdomen are plumbeous at their bases. In some individuals the gray

cast in the abdominal region is pronounced, while in others, the entire ventral surface appears white and the gray can be seen only by parting the hairs. This is probably due to condition of molt.

Males, according to age and season of the year, usually have a brown stain on the white hairs of the ventral mid-line. Howell (1926:16-17) attributed such a stain in the bushy-tailed woodrat to action of sebaceous glands in the thickened dermal area of the mid-ventral line. He suggested that they functioned as scent glands. Howell (*op. cit.*:214) stated that this glandular area was not present in the representatives of the subgenus *Neotoma* which he studied (*Neotoma albigula albigula* and *Neotoma fuscipes macrotis*). However, Linsdale and Tevis (1951:241) did observe similar brown staining on the dusky-footed woodrat (*N. fuscipes*) and concluded that it was the result of such a glandular area. The stain in *floridana* that presumably also results from a glandular area, becomes more pronounced in older males. It attains a maximum size of one inch in width in the middle of the abdomen and extends from the chest to the anus tapering at either end. The stain generally undergoes a seasonal cycle in intensity. It begins to diminish in August and by October or November, is not pronounced. In February and March, however, individuals are again observed with dark stains. Generally, the greatest extent of staining occurs in June and July. The degree of activity of the glandular area varies considerably between individuals even though all might be old adults. Younger males seldom have intense staining. At least one male that was handled on many occasions did not show the stain. One female was observed with mid-ventral staining similar to that in males.

Hair on the hind feet is white above and slate gray below. The front feet are white, tinged with gray. The tail is sharply bicolor, blackish above, whitish below.

An albino of *osagensis* in the University of Kansas Museum of Natural History (18682 adult female) was obtained four and one-half miles NNE of Welda, Anderson County, Kansas. The pelage is pure white and the collector recorded that it had pink eyes. Melanistic individuals have not been observed.

Posture

When a woodrat is indifferent to its surroundings (see Fig. 3, Pl. 1) the animal rests its weight on its rear feet and sometimes also on the base of the tail. The tail usually extends upward at an angle, but may be straight or arched downward, it may be relaxed resting on the substratum either extended straight or curved. The abdomen usually either touches the substratum or is slightly

raised from it. Both of the front feet are generally touching the ground and sometimes the animal maintains a semi-prone position resting on the elbows. The ears are relaxed but not lying flat on the head. When a woodrat is alert to possible danger, the ears are directed forward, and the pupils of the eyes dilate. The entire body is held tense in a "half-crouch" with the weight still on the rear legs and frequently, one front leg is lifted and held flexed across the chest. The tail remains motionless and extended upward. The vibrissae are usually in motion.

Observations on several captive woodrats and of one free-living rat indicated that the most common position when asleep was on the side with the nose between the front legs. The tail may be in a variety of positions, even bent under the body. The pelage is fluffed up and not sleek as when the animal is active.

A woodrat when angered by another frequently lies prone with the head extended forward. The ears are rigid and directed forward even farther than when the animal is alert to possible danger. When the rat fights, the ears are not held flat. This position may account for frequent damage inflicted on the ears. As the rat prepares for combat the vibrissae move rapidly and the tail is flicked quickly from side to side and occasionally strikes the substratum with considerable force.

Gait

When an adult runs, the body is close to the ground and the tail is straight, sometimes held at an angle of as much as 45 degrees and sometimes held parallel to the ground. Juveniles when running, especially if on open ground, move in a series of bounces with the head held low and directed down. The tail may or may not have an upward curve in it. A woodrat seldom moves in a slow methodical fashion, but usually progresses by alternating short pauses with rapid dashes. Even in darkness running at full speed a rat is able to enter an opening scarcely larger than its own body. When a woodrat climbs on a vertical surface such as a tree it seems to rely to some extent on speed and momentum. Woodrats are proficient climbers, but have never been observed to climb by creeping slowly upward as squirrels often do.

Habitat

General Considerations

The habitat that a woodrat can occupy consists of numerous intricately related environmental factors which function as a unit. To survive the woodrat must withstand extreme environmental

fluctuations which might occur only rarely. If one of these environmental conditions is effectively changed beyond the tolerance of the species, this factor becomes limiting and the animal is forced to adapt, move, or perish.

Both physical and biological factors are important in determining suitable habitat for woodrats. The eastern woodrat is most typically an animal of the eastern deciduous forest, although in some areas it occupies habitats more characteristic of other species. *N. floridana* occupies a wider range of habitats than any of the other species of woodrat, which indicates greater plasticity to respond to factors of the environment. With certain exceptions, woodrats are generally associated with arid rocky regions having xerophytic vegetation. The eastern woodrat occurs in this more typical habitat and also in habitats of the opposite extremes.

Being neither strictly arboreal nor fossorial in habits, a woodrat owing to its size is strongly dependent on the presence of abundant cover in its immediate environment. Under most conditions, woodrats compensate to some degree for this need by constructing their characteristic stick houses that serve as a modifying influence on environmental factors such as extremes of temperature and moisture. Morevor, in many cases, overhead cover protecting the house from severe weather conditions is highly important in determining whether or not the house will be occupied by a succession of woodrats. Such continued occupation is the measure of a successful house site. Furthermore, while foraging for food and seeking mates, the woodrat is more vulnerable to predation unless adequate cover is present. The right kind of cover is essential to provide means of escape from enemies. To escape, the woodrat climbs or seeks shelter in a space small enough to prevent the enemy from entering. The house itself provides effective protection from most predators. If the woodrat is to extend its range and occupy niches within limits of tolerance, the migratory routes must have adequate cover. Seemingly, the critical factor is not kind of cover but amount and structure of cover.

For the woodrat to survive it must have an abundant food supply available, but the versatility displayed by woodrats in their feeding habits indicates that in most instances food is not so critical as cover. In the course of this study, many instances were noted in which foods, identical both in kinds and abundance, were present in two nearby areas one of which was occupied while the other was not. The only discernible difference was in the amount of cover.

Factors such as composition and moisture content of the soil and

physiographical features frequently determine the suitability of woodrat habitat. Only those rock outcrops having numerous deep fissures and overhanging ledges are preferred home sites. In certain areas where soil types are suitable, woodrats prefer burrows for nest sites.

Where stick houses are built, means of support for their construction must be available. Even though shortage of suitable building materials may be overcome by a few individuals, such shortage would prevent the existence of a stable population. Numerous examples of such limitation were observed where only flimsy weed stems were available as building materials. The structure and amount of cover perhaps are the most important environmental factors.

Habitat Relations of the Species

Generally, the eastern woodrat is associated with dense timbered and swampy areas in the southeastern part of its range and when more xeric conditions prevail in the northwestern part, the rat is found in rocky situations such as caves, outcrops, dry rocky hillsides, and intermittent wooded stream courses with sparse vegetation. The greater part of the geographic range of this species lies in the eastern deciduous forest; however, it extends into the grassland of the Great Plains to the westward. In eastern Colorado at the western limit of the species, it lives under conditions of scanty rainfall where vegetation is mostly of xerophytic type. Here the houses usually are associated with cactus (Warren, 1942:209).

At the southernmost edge of the range at Key Largo, Florida, woodrats (*N. f. smalli* Sherman) build houses on the rocky floor of the hammocks (Sherman, 1955:113). In central Florida, houses of woodrats, *N. f. floridana* (Ord), usually are built under willow trees on high ground in swampy areas (Hamilton, 1953:180). Also in central Florida, Hill (1945:88) observed woodrats in a dense swamp adjacent to a slow running creek. Cypress, bay, and gum were the principal kinds of trees. The swamp was only a few inches above the level of the creek and subjected to periodic flooding. Farther north in Levy County, Florida, Pearson (1952:459) reported that woodrats were most abundant in areas of dense shrubs in the ecotone between high and low hammock situations. Pearson further observed that nests are frequently constructed in subterranean chambers. In north-central Florida, Blair (1935:271) and Worth (1950:423) found these rats associated with timbered and swampy areas. Worth (*loc. cit.*) observed them usually in the vicinity of water and reported their distribution to be sporadic in that area.

In the Okefinokee Swamp in southeastern Georgia, Harper (1927: 356-360) reported that woodrats lived in stands of cypress in the watery prairies. He found houses in hollow trees, logs, and stumps, as well as uninhabited buildings. In southwestern Georgia, Harper (1929:84) stated: "A swamp rat, building nests of sticks in vines or on the ground, was reported, and could be nothing else but this species [*N. f. floridana*]". In the vicinity of Charleston, South Carolina, Chamberlain (1928:152) found the same subspecies in a wooded, swampy area. Houses were constructed either on the ground or in tangles of grape and smilax vines up to heights of 15 feet. Hollow trees were also utilized as home sites. Chamberlain (*op. cit.*:153) also noted that their distribution was sporadic. Howell (1921:52-53) found *N. f. floridana* most frequently in wooded bottoms or swamps. In the Prairie Belt and Tennessee River Valley of Alabama he found them chiefly in osage orange hedge rows where they often constructed houses 10 to 15 feet from the ground. Rocky bluffs and cliffs were inhabited where present, and large houses were not built.

In northwestern South Carolina, Coleman (1949:200) found *N. f. haematoreia* A. H. Howell living among granite rocks blasted out of the mountain side in the construction of a highway along a precipitous ledge.

The subspecies *N. f. rubida* Bangs occupies habitats much the same as does *N. f. floridana.* In marshes of south-central Louisiana, Svihla and Svihla (1933:73-74) found this woodrat living on tree islands of palmetto, live oak, willow, and cypress. Houses were built against fallen logs, bases of trees, and up in trees. Uninhabited buildings were favorite sites when available. In eastern Texas in river bottom and hammock country, Baker (1942:343) collected specimens of this race where vegetation was dominated by stands of hardwood and pine timber with a luxuriant undergrowth of shrubs and vines, and he stated: "Woodrats in this region apparently do not build brush houses. Burrows at the bases of trees were the only type of woodrat dens observed." In studying this same subspecies in Liberty and Hardin counties, Texas, Bailey (1905:107-109) found that it lived in the thickest woods and around deserted buildings. He stated: "No trace of the rats was found except under the protecting cover of dense timber, brush, or vine tangles, or in hollow logs, trees, or old buildings . . . at Houma, Louisiana . . . I found these wood rats common in the woods and swamps. Some of the houses were built at the bases of hollow trees, over old logs, or under thick

brush mats, but just as commonly they were placed in the lower branches of trees or in vines 10 to 30 feet from the ground."

The literature contains but little information concerning the habitat of the subspecies, *N. f. illinoiensis* A. H. Howell. Howell (1910:228-229) found this rat inhabiting crevices and caves along the high rocky bluffs of Wolf Lake in southern Illinois. Kellogg (1939:283) thought this woodrat might occur along the bluffs and in swamp bottomlands bordering the Mississippi River in Tennessee.

In the range of the subspecies *N. f. attwateri* Mearns more xeric conditions prevail. Otherwise, the habitat is somewhat similar to those of the other subspecies; often the rat is found along stream courses. In south-central Texas, Lay and Baker (1938:418-421) found *attwateri* using underground dens along wooded stream banks. One individual was living in a burrow made by an armadillo (*Dasypus novemcinctus*). Post oak (*Quercus stellata*) and winged elm (*Ulmus alata*) were the principal trees. In the same area, Strecker (1929:220) had earlier found *attwateri* occupying caves and crevices along wooded stream banks. Farther west, in Kerr County, Texas, Bailey (*op. cit.*:110) states that this subspecies ". . . lives in a rocky half-forested region. It makes its house sometimes among the rocks, piling up its rubbish in a broken cliff, rock piles, or old stone walls, and sometimes in the woods at the base of a tree, under a brush pile, in some old cabin, or along the river in heaps of flood drift."

Habitat in Eastern Kansas

Present habitat of the woodrat in eastern Kansas is divisible into two principal types; the osage orange, *Maclura pomifera* (Raf.), hedge-row habitat type, which is the more widespread, and the rock outcrop type of habitat. Stone fences, upland woods, wooded stream courses, shrubby hillsides, and uninhabited buildings constitute habitat types of less importance.

According to Livingood (1914:3), the original range of the osage orange tree covered little more than 10,000 square miles. Its northern limit was near Atoka, Oklahoma, and its southern limit somewhat south of Dallas, Texas. It extended into northwestern Louisiana and southwestern Arkansas. Its broadest east-west extent, approximately 120 miles, was in Texas. Between 1865 and 1939, 39,400 miles of single-row osage orange hedge rows were planted by farmers in Kansas (Yearbook of Agriculture, 1949:783). The growth habit of this tree, especially as modified by trimming,

makes hedge rows excellent habitat for woodrats. Leaves and fruit or "hedge balls" furnish an ample supply of food. As the planted hedge rows matured and the rather rapid destruction of native timber by man took place, woodrats seemingly shifted from wooded stream courses to this more favorable new habitat. In northeastern Kansas, Kellogg (1915:182) found that woodrats preferred living in tangled underbrush in the lowlands along timbered streams. They built houses around hollow logs or under overhanging roots of trees along creek banks. In the course of this study few occupied houses were observed in this situation. Woodland along several streams in Greenwood County in southeastern Kansas was investigated for the presence of woodrats in 1954; none was found although they were numerous in hedge rows of that area. Changes brought about by man in cutting of timber may have unfavorably altered habitat along stream courses.

The presence of a hedge row does not necessarily create conditions favorable for occupancy by woodrats. In eastern Kansas in 1955 unoccupied hedge rows are more numerous than those that are occupied. In some areas, this is not due to absence of woodrats but is the result of the condition of the hedge rows. Farmers frequently trim the trees after they reach a large size, in order to gain additional ground for cultivation of crops. Many farmers destroy the hedge rows because of their tendency to draw water from the soil, even at considerable distances from the row. In an untrimmed row the limbs grow from the trunk close to the ground and bend, arching outward and downward to form a canopy. The growth is so thick and the thorny limbs so formidable that it is usually necessary to remove several limbs before reaching the base of the tree (Fig. 1, Pl. 2). When trees are young, trimming, or browsing by cattle results in a thick bush. Under these influences trees in hedge rows usually have multiple trunks branching close to the ground, well suited to support houses of woodrats. The wood is extremely tough and durable and limbs from these trees last for many years before rotting. Houses constructed in hedge rows are always made mostly from sticks of the osage orange tree. Limbs trimmed by farmers are frequently left in piles providing a source of building material, and on occasion houses are constructed in the brush piles. Many excellent escape routes are available owing to the close proximity of the trees in a hedge row. When a house is disturbed, the rat, in most instances, dashes from the house up into a tree. If pursued further, it can travel with ease from tree to tree. Rats are

PLATE 1

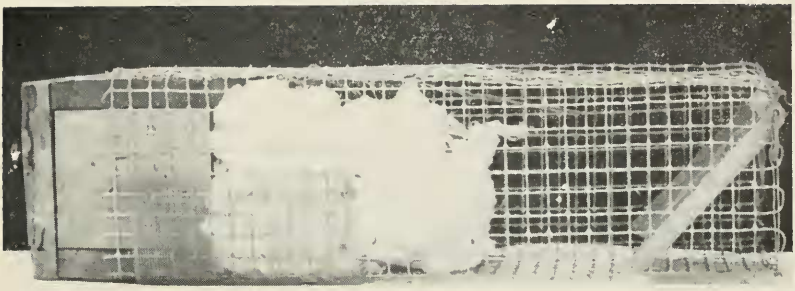


FIG. 1. Live-trap containing wooden nest box. A captured woodrat has pulled cotton from nest box to form a nest. × approx. ⅕.

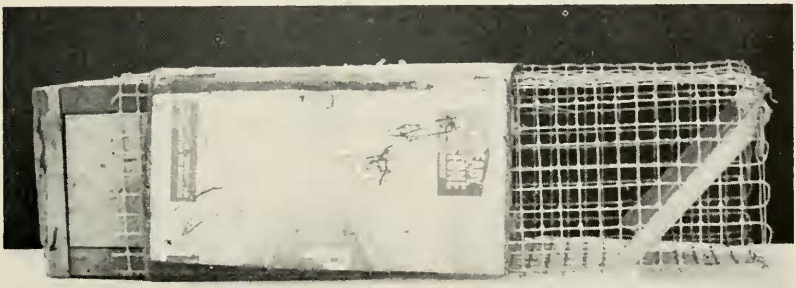


FIG. 2. Metal can around live-trap to provide protection from rain and snow. × approx. ⅕.

FIG. 3. An adult, female, eastern woodrat (raised in captivity—from parents captured 4½ mi. NNE Lawrence, Douglas Co., Kansas), illustrating typical posture when not alarmed. December 4, 1953. × approx. ⅓.

PLATE 2

Fig. 1. A hedge row that has been allowed to grow, providing excellent woodrat habitat, with adequate cover and sites for houses. Jefferson County, July 27, 1954.

Fig. 2. A hedge row 7 mi. E Eureka, Greenwood County, Kansas, supporting a large population of woodrats. Note the lack of ground cover away from the row. Woodrats living here were entirely dependent on the row for food and shelter.

Fig. 1. An isolated osage orange tree, 6 mi. N Madison, Greenwood County, Kansas. There was a large woodrat house up in the tree, which furnished all essentials for the existence of the woodrat. No other woodrat could be located within a half-mile radius.

Fig. 2. A rock fence, one of the minor habitat types for woodrats in eastern Kansas where such fences are fairly common. Five mi. W Lawrence, Douglas County, Kansas, July 27, 1954.

FIG. 1. Tongues of forest along small stream courses in the Flint Hills, 8 mi. S Manhattan, Riley County, Kansas, in terrain dominated by grasses. July 25, 1954.

FIG. 2. Thickets along a stream course in the Flint Hills, 7 mi. S Manhattan, Riley County, Kansas, a habitat favorable for woodrats. July 25, 1954.

FIG. 3. Site of woodrat houses in the Flint Hills among limestone boulders of "rimrock" with thickets of dogwood. Wabaunsee County, Kansas, July 25, 1954.

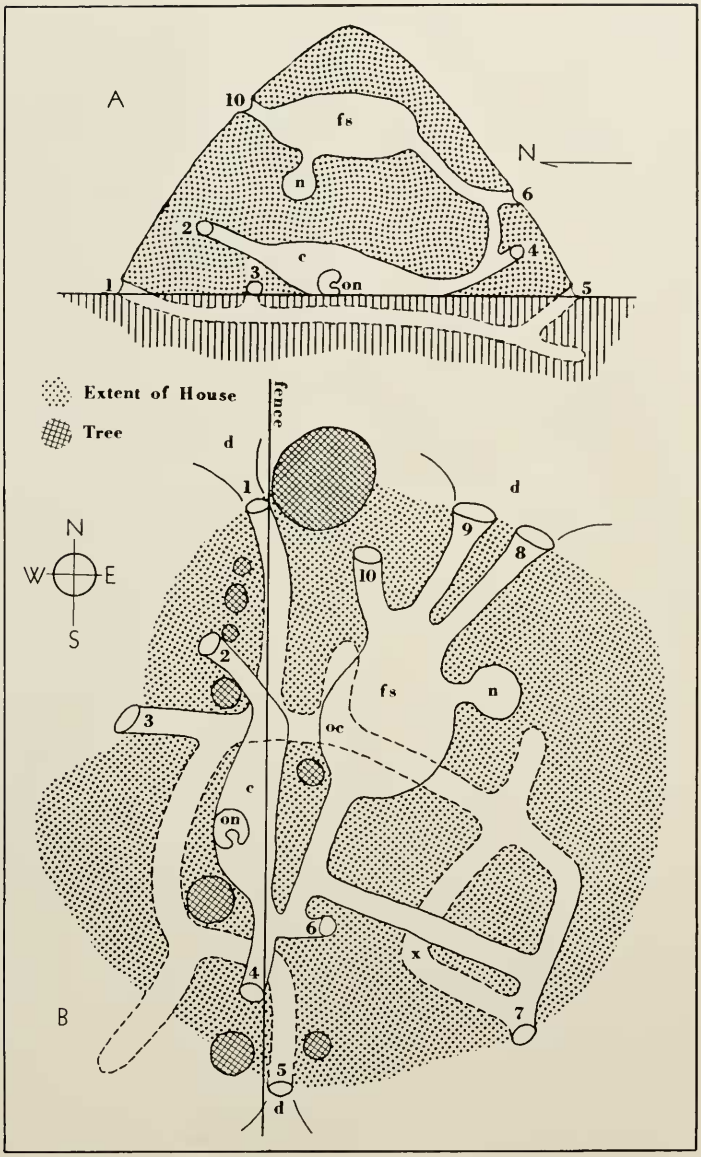
PLATE 5

FIG. 1. One of the smaller houses in the hedge row discussed on page 566. The house was 821 feet south of the southeast corner of the Reservation on private land. November 17, 1954.

FIG. 2. House in a hedge row; note use of trees as support allowing vertical growth of the house. The house is 761 feet south of the south boundary of the Reservation. November 17, 1953.

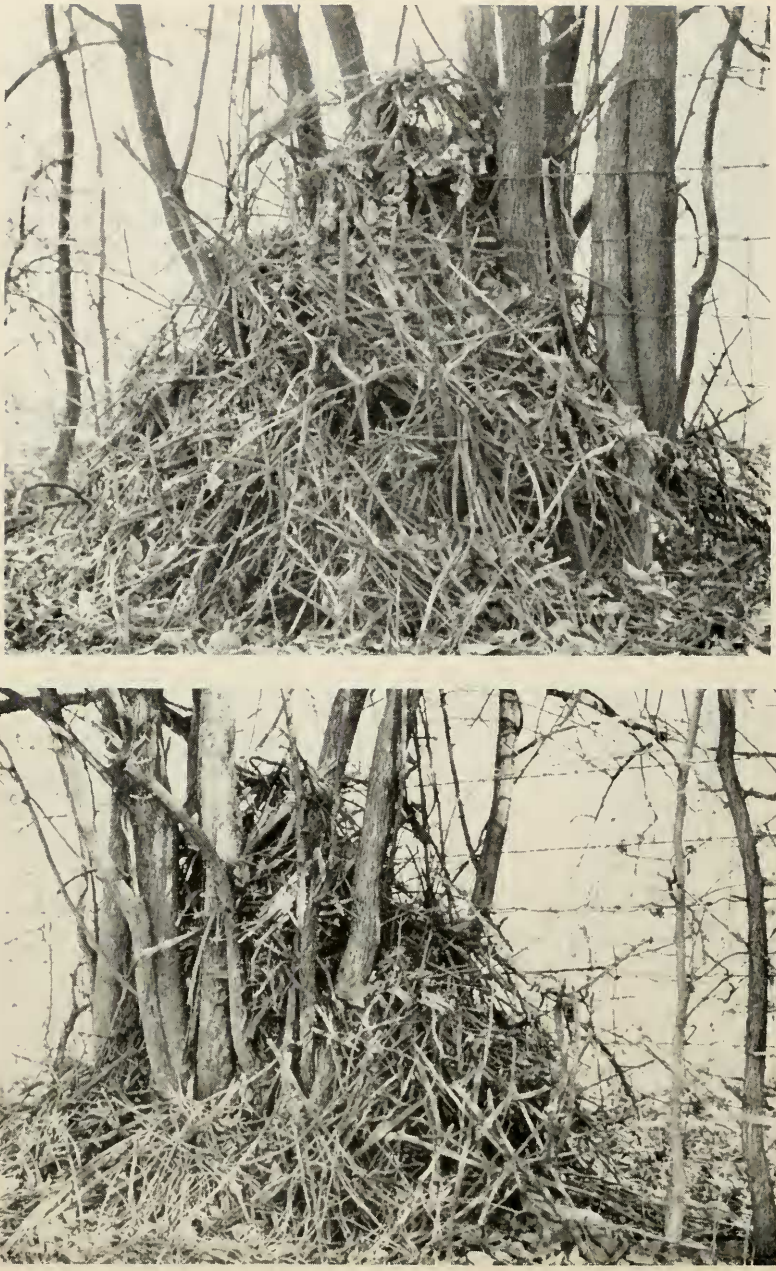
FIG. 1. View of a part of the study area. The outcrop of rock extends along the horizon. July 27, 1954.

FIG. 2. West side of house shown diagrammatically in Plate 7. Southeast corner of Reservation on private land. November 17, 1953.



(A) Diagrammatic side-view of a house typical for hedge rows. (B) Floor plan of the house drawn to the scale of one inch to eighteen inches. fs = food store; d = debris from inside the house; n = nest chamber; on = unused nest chamber; c = chamber; oc = osage orange cuttings; x = site of opened coffee beans and walnuts. See Fig. 2 of Plate 6, showing same house.

PLATE 8



Two views of one house from opposite sides of the hedge row illustrating use of both fence and trees for support. House was 921 feet south of the southeast corner of Reservation. November 15, 1953.

PLATE 9

A woodrat house in a hedge row 15 mi. E Talmage, Dickinson County, Kansas, five feet from the ground. July 28, 1954.

PLATE 10

FIG. 1. A house at the edge of an old well three feet from the trees of a hedge row, 3 mi. S, 1 mi. W Hamilton, Greenwood County, Kansas. July 27, 1954.

FIG. 2. A long-occupied house on the Reservation part of the eastern outcrop on the study area. The overhanging ledges provide excellent protection from adverse weather. February 14, 1955.

FIG. 1. A house in the pastureland part of the study area and constructed of common ragweed stems. February 14, 1955.

FIG. 2. The low rock fence separated the woodland and pastureland parts of the study area. A house was at the base of the old elm snag. A tangle of wild grape vines covered most of the house. February 14, 1955.

FIG. 1. A woodrat house on a south-facing slope in the Flint Hills, 7 mi. S Manhattan, Riley County, Kansas. Note density of vegetation on slope. July 30, 1954.

FIG. 2. A well-built, cone-shaped house on a wooded slope in the Flint Hills, 7 mi. S Manhattan, Riley County, Kansas. Fragrant sumac in front of the house provided support and permitted such a shape. July 30, 1954.

protected also by the overhanging limbs while foraging on the ground.

Woodrats are seldom found in isolated or frequently trimmed hedge rows. They are most numerous where the rows are interconnected over large areas. An area investigated in Greenwood County in the summer of 1954, was found to include excellent habitat for woodrats (Fig. 2, Pl. 2); hedge rows were numerous and encompassed all sides of several sections of land. In most instances, however, only a part of each mile of row was suitable for houses. Three interconnecting rows, each one mile in length, were investigated for the presence of woodrats. In each case, approximately half of the row was suitable for houses although the remaining parts were dense enough to allow traveling. Thirteen houses were found in each of two rows and ten houses in the third; a total of 36 houses in one and one-half miles of rows. Judging from the sign around the houses, nearly all appeared to be occupied. In a similar area in the same county, eight occupied houses were found in another row approximately one-fourth mile in length. Since hedge rows were planted, the osage orange has spread so that now in many places this tree along with honey locust (or honey-shuck, *Gleditsia triacanthos* L.) forms woodland of considerable size where original trees have been cut or original prairie has been destroyed. Woodrats have been found in such woodland of osage orange and locust. Houses are built at the bases of trees or up in them.

Because rock outcrops furnish suitable cover both for houses and for foraging, requirements are more easily satisfied near rock outcrops than they are in hedge rows. Usually the houses are not so large in this situation as in the hedge rows.

Rock fences prepared in the process of clearing land for cultivation are frequently utilized by woodrats as house sites (Fig. 2, Pl. 3). Shrubby plants which commonly grow along these fences especially fragrant sumac (*Rhus aromatica* Ait.) furnish good support for the houses. Frequently, these fences are used as travelways.

Habitat in the Flint Hills is restricted. The vegetation is predominantly blue-stem grass (*Andropogon Gerardi*). Extensions of the forests of eastern Kansas are found along stream courses and on the valley slopes (Figs. 1, 2, Pl. 4). On the rocky slope north of a small stream seven miles south of Manhattan, Riley County, Kansas, in the summer of 1954, 11 houses found within a distance of approximately 100 yards were mostly low and spreading, not conical as are most houses in hedge rows. Some of the houses utilized rocks

for support while others were constructed around the bases of fragrant sumacs. The trees were principally burr oak (*Quercus macrocarpa*) and chestnut oak (*Q. Muehlenbergii*). There were a few scattered honey-shucks (*G. triacanthos*) and American elms (*Ulmus americana*); the understory was composed of dogwood (*Cornus Drummondi*), redbud (*Cercis canadensis*), fragrant sumac (*R. aromatica*), and coralberry (*Symphoricarpos orbiculatus*). The south slope lacked the dense understory found on the north slope, and only two old unoccupied houses were found. Three occupied houses were found along an exposure of large limestone boulders at the crest of a small hill in another area of the Flint Hills (Fig. 3, Pl. 4). Dogwood formed a low dense thicket among the rocks. Woodrat houses were built on the boulders and utilized some of the dogwoods for vertical support. The surrounding area was entirely open grassland except for a few dogwoods on the hilltop.

Buildings such as barns, uninhabited houses, and storm cellars, are favorite haunts for woodrats. In some cases, sticks and trash are brought from the outside in great amounts and used to construct houses. Woodrats occasionally invade barns and garages that are in use. Their presence is easily detected and most generally, attempts are made to remove them. In some circumstances they gather and store large amounts of fruit or nuts considered valuable by the owner of the building.

Study Area

While certain aspects of the study, such as collecting specimens for laboratory use and dismantling houses, were carried out in other locales, live-trapping was confined to an area of approximately 58 acres in northeastern Douglas County. Nine acres of the study area were on the University of Kansas Natural History Reservation and the remainder on adjacent privately owned farmland. Nearly all the area was woodland (Fig. 1, Pl. 6). Douglas County is in east-central Kansas in the ecotone between eastern deciduous forest and western grassland.

Woodrats occurred locally in colonies where habitat conditions were optimum, and were most abundant along a limestone outcrop approximating the 1050-foot contour. This outcrop, an exposed edge of a stratum of Oread limestone underlying the shallow glacial till of the hilltops, constitutes a prominent physiographic feature of the Reservation and surrounding areas. Approximately 20 feet below the level of the hilltops is another stratum of limestone, but it is not exposed to the extent of the upper one. For purposes of

convenience, no distinction is made between the upper and lower outcrops in following discussions. The upper outcrop varies in thickness from two to six feet. The face of the outcrop is deeply fissured, cracked, and has numerous ledges of overhanging rock. Boulders and smaller rocks broken from the outcrop are strewn down the hillside (Fitch, 1952:8).

Live-trapping was done along a 750-foot "eastern part" of a southwestern exposure of a limestone outcrop and along a 650-foot "western part" of the outcrop separated from the first by approximately one-fourth mile of woodland. Both were parts of the same outcrop, but the connecting stretch passed through an overgrazed pasture which was unsuitable woodrat habitat. The continuous eastern part was divided between three areas long under different ownership and subjected to land uses that had resulted in differences in vegetation: a 400-foot stretch on the Reservation, a 100-foot stretch in adjoining woodland, and a 250-foot stretch in open pastureland. The latter part was the only part of 1500 yards of outcrop in the overgrazed pastureland that was inhabited by woodrats. After extending through the pastured area, the outcrop where the western part was located again entered woodland. At the western part, approximately half the distance of the outcrop had an eastern exposure; the remainder had a southern exposure. A rock fence separating the woodland from the pastureland and connecting the eastern and western parts of the outcrop, was utilized to a certain extent for house sites and as a travel route.

Plants were counted on a series of quadrats taken along the eastern part in July, 1952, to determine differences in vegetation as reflected by varying land uses. The results are given in Table 1. The Reservation has been protected from grazing and cultivation since 1948, and along the outcrop and on the hillside below is an extremely dense thicket of dogwood, with also more kinds of smaller plants than on the remaining two portions of the eastern part. Important food plants rank higher in terms of abundance. A few hackberry trees (*Celtis occidentalis* L.) occur along the outcrop.

The woodland part of the study area was grazed by cattle. Trees were principally osage orange with scattered honey-shucks and elms. According to Mr. J. F. Morgan, a life-long resident, there were no trees here except for a few on the crest of the hill at the turn of the century. Coralberry began invading the hillsides by 1920 and osage orange had appeared in the late twenties. At

present coralberry is the dominant small plant. Ground cover is not so dense along this part of the outcrop as along the part on the Reservation.

Plants indicative of overgrazing dominated the pastured area. These plants rank low in palatability to woodrats. Trampling of

Table 1. Differences in Vegetation, Reflecting Varying Land Usage, Along the Eastern Part of the Outcrop. Figures are Based on Counts from 75 Quadrats

Species	Percent of total count		
	Reservation part	Woodland part	Pastureland part
White Snakeroot (*Eupatorium rugosum*)	69.8	.5	absent
Dogwood (*Cornus Drummondi*)	7.6	11.2	.5
Bittersweet (*Celastrus scandens*)	5.7	absent	absent
Goldenrod (*Solidago* sp.)	5.4	3.3	absent
Hackberry (*Celtis occidentalis*)	2.3	17.4	3.4
Virginia Creeper (*Parthenocissus quinquefolia*)	2.1	.2	.3
Avens (*Geum canadense*)	1.5	2.4	absent
Fragrant Sumac (*Rhus aromatica*)	1.3	.2	absent
Sunshine Rose (*Rosa arkansana sulfata*)	1.3	absent	absent
Dropseed (*Muhlenbergia Schreberi*)	.8	absent	absent
Greenbriar (*Smilax tamnoides*)	.6	.4	absent
Smooth Sumac (*Rhus glabra*)	.5	1.8	absent
Winter Grape (*Vitus vulpina*)	.3	absent	absent
Leadplant (*Amorpha canescens*)	.2	absent	absent
Compass Plant (*Silphium laciniatum*)	.2	absent	absent
Poison Ivy (*Rhus radicans*)	.2	absent	absent
Coralberry (*Symphoricarpos orbiculatus*)	.2	59.2	4.6
Wild Licorice (*Galium circaczans*)	absent	2.5	absent
Bush Clover (*Lespedeza* sp.)	absent	.4	absent
Mullein (*Verbascum Thapsus*)	absent	.2	absent
Ironweed (*Vernonia Baldwini interior*)	absent	absent	44.2
Common Ragweed (*Ambrosia artemisiifolia elatior*)	absent	absent	33.1
Marijuana (*Cannabis sativa*)	absent	absent	11.0
Sunflower (*Helianthus annuus*)	absent	absent	2.2
Snow-On-The-Mountain (*Euphorbia marginata*)	absent	absent	.5
Black Nightshade (*Solanum nigrum*)	absent	absent	.2
Total count	609	552	644

horses and swine had resulted in an almost complete disappearance of plants in the vicinity of the outcrop. This lack of ground cover coupled with lack of desirable food items probably accounts for the scarcity of woodrats along the part of the outcrop located in the pastureland.

Moisture Requirements

Observations on woodrats in captivity indicate that in nature the need for water, either free or from green plants, is important. The water content of fresh lettuce given regularly will satisfy the needs of captives, but foods deficient in moisture content must be supplemented by a supply of water. Woodrats deprived of water in summer dehydrate rapidly and lose weight. When free water is given to thirsty captives, they have frequently been observed to drink as much as five minutes without pausing.

In a 24-hour period, two captive rats having access to lettuce which had lost most of its water content consumed 28 and 22 cc. of water. The maximum temperature was 92° and the minimum was 73°. In the second 24-hour period, they consumed 34 and 36 cc.; maximum temperature was 93° and the minimum was 76°. The food was dry dog biscuits. In the third period with the same food, they consumed 64 and 58 cc. of water. The maximum temperature was 92° and the minimum was 73°.

In nature, water requirements are probably satisfied from dew, rainwater, and green plants. Much vegetation died in the drought summers of 1952 and 1953, and there were many consecutive nights without a trace of dew. Seemingly, it would have been difficult for woodrats to meet their water requirements. Moisture deficiency possibly was an important factor in the rapid decline of the population in the woodland section of the study area; however, individual records in 1952 are not complete enough to permit conclusions as to effects on their general health.

The mulch and soil beneath woodrat houses are normally moist even though soil is dry elsewhere. Houses dismantled in 1953 were extremely dry throughout, and the soil beneath them was dry to a depth of more than six inches. Throughout some houses there were heavy deposits of dust which may have been harmful to the occupants.

Owing to the better overhead cover, heavy amounts of rainfall probably do not handicap woodrats dwelling at outcrops as much as those living in stick houses in open woodland. Record amounts of rainfall in 1951 resulted in flooding but seemingly had little effect on adult woodrats; however, young may have been harmfully affected.

Relation to Heat

Within the protection of their houses, woodrats are well insulated and are able to withstand hot weather. Excessively high temperatures were common in the summer of 1954. Three females were

kept in captivity in sheltered outdoor cages where a maximum-minimum thermometer registered temperatures as high as 112° F.; all survived. On several occasions, however, rats exposed to direct sunlight while in live-traps were found dead even though the air temperature was not excessively high. Others not dead were in a weakened condition and probably died after release because they were never caught again. Seemingly, after exposure to high temperatures they are not able to recover. The usual signs of heat prostration are wet fur around the mouth, rapid breathing, extreme lethargy, and inattentiveness to surroundings.

Houses constructed under overhanging ledges of outcrops are protected to a large degree from direct sunlight and the temperature is much more stable inside the house than outside both in summer and in winter. On August 29, 1953, an outdoor-indoor type thermometer was used to record temperatures every hour for 12 hours within a house constructed under an overhanging ledge, and at the same time, this thermometer recorded outside air temperature. Hourly readings, made from 7 A. M. to 7 P. M. inclusive, were as follows, figures in parenthesis representing air temperatures outside the house: 76, (79), 78 (79), 82 (82), 85 (88), 90 (92), 92 (95), 94 (99), 96 (101), 98 (106), 99 (106), 96 (103), 93 (94), 91 (92). Sunlight reached the house for a short interval in the day.

Maximum-minimum temperatures in consecutive 24-hour periods were also recorded for several houses along the outcrop in different seasons of the year. One maximum-minimum thermometer was inserted as far back under the ledge as possible among the sticks of the house and another one was set up in an outside shelter. Temperatures were recorded approximately the same time each morning. Table 2 gives the results recorded at one house in a warm period while Table 3 gives the results recorded at the same house in a cold period. In the hottest part of the day the temperature within the house remained 5 to 16 degrees cooler than outside air temperature; however, owing to the heat retaining qualities of the rock, minimum inside readings were somewhat higher than outside readings. In cold weather the latter situation is advantageous to woodrats.

Woodrats that remained in a live-trap throughout the night were able to maintain their body temperatures even though the air temperature was either cold or hot. Table 4 shows rectal temperatures taken in May and June, 1953, compared to air temperatures taken at the time the rat was removed from the trap.

Relation to Cold

Woodrats provided with adequate food and nesting material are able to withstand considerable cold when in live-traps, and have been known to pass the night without any ill effects at temperature as low as 22° F. On October 18, 1952, an adult male was caught in a live-trap that was not provided with either a nest box or nesting material. The temperature dropped to 30° F. during the night.

TABLE 2. COMPARATIVE MAXIMUM-MINIMUM 24-HOUR TEMPERATURE RECORDINGS INSIDE A WOODRAT HOUSE AND OUTSIDE THE HOUSE IN A PERIOD OF HOT WEATHER.

Date	Temperature recordings (F.)			
1953	Maximum readings		Minimum readings	
	Outside	Inside	Outside	Inside
September 6	85	80	62	67
September 7	91	81	63	65
September 8	88	76	62	66
September 9	92	84	68	69
September 10	97	90	70	72
September 11	100	94	67	72
September 12	102	86	56	64

TABLE 3. COMPARATIVE MAXIMUM-MINIMUM 24-HOUR TEMPERATURE RECORDINGS INSIDE A WOODRAT HOUSE (SAME HOUSE AS IN TABLE 2) AND OUTSIDE THE HOUSE IN A PERIOD OF COLD WEATHER.

Date	Temperature recordings (F.)			
1953	Maximum readings		Minimum readings	
	Outside	Inside	Outside	Inside
February 9	73	74	38	41
February 10	74	64	40	42
February 11	70	56	22	34
February 12	57	50	17	27
February 13	64	58	36	34
February 14	68	62	52	50
February 15	80	73	61	59
February 16	68	66	33	42
February 17	66	57	37	42
February 18	69	62	37	41
February 19	68	63	46	47

Table 4. A Comparison of the Body Temperatures, and Air Temperatures at the Trap Site, in Warm Weather and in Cold Weather of Several Live-trapped Rats.

Date	Sex	Body temperature (F.)	Air temperature (F.)
WARM WEATHER			
May 30, 1953	Female	103	101
June 3, 1953	Female	101	83
June 3, 1953	Female	97	83
June 4, 1953	Male	97	86
June 7, 1953	Female	101	88
June 7, 1953	Female	101	88
June 8, 1953	Male	99	77
June 9, 1953	Female	101	91
June 9, 1953	Female	104	96
June 10, 1953	Male	97	77
June 13, 1953	Male	101	80
June 14, 1953	Female	100	85
COLD WEATHER			
December 14, 1953	Male	95	26
December 14, 1953	Female	97	28
December 15, 1953	Female	97	28
December 15, 1953	Male	97	32
January 6, 1954	Male	95	34
January 6, 1954	Male	94	28
January 6, 1954	Female	98	28
January 7, 1954	Female	93	28
January 7, 1954	Male	95	28
January 8, 1954	Female	93	28
January 8, 1954	Female	95	49

The body temperature of the rat when taken after removal from the trap was 98° F. There was no apparent harm to the rat which survived in the area for five months thereafter. When provided with cotton nesting material, a rat in a live-trap would form a nest which almost entirely enclosed its body. In many instances when the temperature was low, the rats were observed to shiver much as humans do when they are chilled.

Probably woodrats are not harmed to the same extent as are some other small mammals by winter weather conditions such as prolonged accumulations of snow, chiefly because of the protective nature of their houses and the stored food supply. Extreme low temperatures when of short duration are not harmful. Rats in

captivity have withstood temperatures as low as —7° F. without damage provided they had ample food and nesting material, but under certain conditions extremes of weather can cause heavy mortality.

Table 4 includes rectal temperatures compared with air temperatures in cold weather. It will be noted that body temperature tends to range slightly lower in cold weather.

Relation to Light

Woodrats are rarely seen in daylight. On a warm winter day a woodrat was reported seen at the site of an old quarry on the Reservation sunning itself on a rock. On another occasion, I observed one dust bathing approximately two feet from its house in a brush pile. The animal had sufficient protection but was in mid-afternoon sunshine. On June 2, 1953, at 3:15 P. M., a young woodrat (estimated to weigh 75 grams) was seen outside a house into which it escaped when I came into sight. When a woodrat is released from a live-trap, it usually pauses briefly, getting its bearings perhaps, and then it almost always runs to the nearest place that furnishes some shade. Ordinarily these rats exhibit an extreme dislike for bright sunlight. However, one that is hungry may venture to sunlight long enough to clip off a plant and take it to shelter to be eaten.

On dark rainy nights woodrats are usually more active than on clear nights. Seemingly, this is directly the result of increased darkness. However, the rats dislike getting wet, and forage in slack periods in the rain. In October, 1954, I had an opportunity to observe the behavior of a woodrat on a rainy night. An adult male lived in the garage on the Reservation and had constructed a nest behind some large pieces of fiber board. This nest was not covered by sticks and the animal could easily be observed at night with a red light. Even in the day it remained dark enough so that a light was necessary to see the rat. On the afternoon of October 21, 1954, a live-trap was placed in the garage. By 7:45 P. M. the rat was in the trap; he was marked and released whereupon he went directly to the nest. It was not yet totally dark. Soon rain began and by 10:30 P. M. the rat had not left the nest to forage. At 11:30 P. M. rain had stopped and the rat was not in the nest. The following night was clear. The rat was in the nest at 6:35 P. M. but one hour later he was gone, and had not returned by 9:00 P. M. when observations were halted. This indicated that even in darkness, woodrats dislike foraging in the open when it is raining.

Houses

General Character

Shape, size, and construction of woodrat houses vary according to the sites where they are located. In eastern Kansas, woodrat houses are constructed almost exclusively of sticks, but if sticks are lacking in the immediate vicinity, large weed stems may be substituted. Houses in some locations are relatively inconspicuous. Those bordering small creeks frequently resemble drift material. Woodrats sometimes actually incorporate and elaborate such a drift pile into a house. Volume of houses varies considerably and is related to location. Some consist of no more than a few sticks scattered over one end of a hollow log or around a rock crevice, and seem to serve no purpose, beyond the expression of the collecting instinct. Exceptionally large houses may be up to nine feet in diameter, and four to five feet high. Shape depends on location; if a vertical object is available for support the house will be cone-shaped, but in the absence of such support, the house is flattened and considerably broader at the base. Growth of the house is always chiefly vertical as long as support is present, but when this is lacking, the house broadens at the sides and base. This woodrat characteristically adorns the top of the house with such objects as rocks, dung, pieces of bark, broken glass, bones, or any other strange object which may be in the vicinity.

Uses

When any other suitable cover such as deep crevices, or burrows are lacking, the house is of definite survival value for a terrestrial mammal the size of a woodrat. The house is an environmental adaptation serving as a retreat where many activities can be carried on under sufficient protection from enemies or weather conditions. As long as a woodrat is at home it is relatively safe from natural enemies, but vulnerability increases greatly when it moves away from the home shelter. Houses also serve as a means of escaping certain types of enemies. As the woodrat is primarily nocturnal in habits, the house serves for a daytime retreat where the animal can sleep, eat, or clean itself. Houses are vitally important in increasing survival of the young especially when they are temporarily left alone. Abandoned houses are frequently utilized as temporary shelter for woodrats moving from one area to another thus increasing the likelihood of interpopulation flow which is important in colony stabilization. The house, if in good condition, furnishes

protection from rain, snow, and excessive heat. Well-maintained houses can withstand considerable rain before becoming wet throughout. The instinct for storing food is highly developed in woodrats. The house is used as a storage place where green plant material will remain fresh for a considerable length of time; the food is partly protected from other animals which might pilfer it.

Signs of Occupancy

The general appearance of the house cannot always be relied on to ascertain whether or not it is occupied. In general, a house in a hedge row is peaked if occupied. Flattened houses in such situations are rarely inhabited although they may be used as temporary shelter. Many occupied houses that are low and flat have been observed in other situations. Recent droppings indicate occupation; they are usually in piles of varying sizes in one or two places just outside the house near the base or several feet away at a favorite site. Droppings less than 24 hours old are soft and almost black; those several days old turn progressively more brown, harden, and decrease in size as desiccation takes place. Debris or pieces of recently collected food at entrances usually indicate occupation. Under certain conditions, well-worn trails, void of leaves or other debris, leading from the house are good evidence that it is inhabited. In warm weather houses not in use usually have spider webs over the entrances although a period of time may elapse before this occurs. The appearance of sticks on the surface, whether recently collected or not, could not be used as a criterion of occupancy. There has been no evidence that sticks are collected by gnawing them from larger limbs or trees, but to the contrary, it is my impression that they are collected on the ground from fallen twigs or rotting limbs. Large weed stems are perhaps gnawed into smaller pieces but these are seldom used.

Structure

Most houses of woodrats in this area are basically similar although there are differences in degree of complexity and arrangement; houses along outcrops form an exception to this. Because of the intensive use of fissures and crevices, systems of tunnels are not developed. A nest chamber could not be found in either of two such houses which were dismantled. In a given area, houses in close proximity to one another will vary in extent of tunneling both above and below ground. Tunnels are often dug in the matrix of old droppings, rotted wood, and discarded food material which ac-

cumulates to depths of six inches or more beneath the house. This material may be compacted so that the entire layer resembles a thick sheet of cork. The location of the nest chamber varies from ground level to a level considerably higher. Frequently, the nest is beneath roots or in the hollow base of a tree incorporated into the house. Size of the nest chamber varies but little. Most nests are spherical and approximately six inches in diameter; however, the inner cavity varies according to size of the woodrat using it. The store of food is usually in one mass in the upper part of the house, but sometimes is divided into two or more parts. There also are one or more places where debris from inside the house is carried outside the house. Usually there are one or more places where the occupant habitually defecates; this may be just inside the house or several inches away.

Numerous houses were dismantled in order to study their structure. A large house located in the hedge row which grew on private land adjacent to the southeastern corner of the Reservation is here described as representative of those occurring away from rock outcrops in this area. A diagrammatic side view and floor plan of a house occupied by a subadult female is given on Plate 7.

This house also relied on support of both osage orange trees and a cattle fence (Fig. B, Pl. 7). Osage orange sticks were used mostly for building materials, but several ragweed stems were scattered over the surface. In the north-south direction, the house was 64 inches wide at ground level and 18 inches at the top. The house was 35 inches high.

There were ten well-defined entrance holes, six at ground level the others part way up on the sides. There were accumulations of old droppings and bits of osage orange fruit expelled from the house about entrances 1, 5, 8, and 9. A mound of soil free from debris, where the occupant probably took dust baths, was at entrance 3. Tunnels passed through the soil and a six-inch compacted layer of midden, droppings, and decomposed wood on which the house rested. The depth of this basal layer of midden indicated that the house was old.

The food store in this house, situated only a few inches below the top, measured 21 inches long and 16 inches high. The bulk of the stored food consisted of osage orange leaves, but a few pieces of the fruit were also found. There was a small amount of old leaves collected the previous season. A platform in a small chamber formed by the convergence of three tunnels at the north end of the food

store had an accumulation of droppings, empty osage orange seeds, and leaf fragments. Indications were that most of the feeding was done on this platform. The occupant had been removing food from this end of the cache only.

The nest was below the food store but not at ground level, and sticks of the house supported it. It was globular, six inches long and five and one-half inches wide; the inner cavity was four inches deep and three inches wide. The nest was made from shredded bark and smaller amounts of grass blades.

Entrance 2 was 17 inches from the ground up on the side of the house, and led to an enlarged chamber at ground level which measured 19 inches long and six inches high. Entrances 4 and a branch from 6 extended down to the south end of this chamber. Old droppings formed the floor of the chamber. A few pieces of osage orange fruit with the seeds removed and an old misshapen nest were found within the chamber. Entrances 1, 3, and 5, led to subsurface tunnels. The debris about 1 and 5 probably resulted from the excavation and enlargement of these tunnels. The bases of the hedge trees were undermined by these subsurface tunnels.

Tunnels leading from entrances 1 and 3 joined to form a system which emerged at entrance 7. At the place where a short blind tunnel branched off the main tunnel, several new cuttings of young osage orange twigs averaging three inches in length were found. A small rock, four ventral scutes from the shed skin of a snake, and a piece of a scat of an opossum, were near the cuttings. The tunnel passed almost straight beneath the house and near the east side branched into three tunnels, one ending blindly, and the other two again joining at entrance 7. In one of these branches several opened coffee beans, three opened walnuts, and two grains of corn were found. There were no conspicuous trails leading from this house; seemingly the occupant utilized the branches and trunks of the fallen trees for traveling.

Three additional houses located in this hedge row were studied. One had only three entrances and there were no distinct trails leading from the house (Fig. 1, Pl. 5); however, there was an extensive system of subsurface tunnels. The food cache was again near the top and the nest chamber was a few inches below. The nest rested on a platform of droppings and food debris; a short tunnel led to the food store.

Well-defined trails several feet in length ran along the hedge row from either end of another house. This house had seven en-

trances. Narrow strips of bark up to 31 inches in length had been pulled from a dying tree and placed on the sides of this house (Fig. 2, Pl. 5).

The third house also had only three entrances and the tunnel system was simple (Plate 8). Two of the entrances were connected by a runway and a branch of this led to the nest. Because the nest was immediately below the food store and at one end, a runway was not necessary to connect the two. The nest was five inches across and four inches deep on the outside; the entrance measured two and one-half by two inches and the cavity three inches deep. The small size of the subadult female (214 grams) occupying this house accounts for the small size of the entrance to the nest. The tunnel leading from the third entrance was so ill-defined that it could not be followed. One notable difference observed at this house was that the only fecal depository was deep within the house.

A large, excellently constructed house dismantled on January 31, 1953, demonstrated preference for a brush-pile site over a hedge-row site. Four small osage orange trees about 15 feet in height at one end of a hedge row had been uprooted in the construction of a cattle fence. Each of the trees had more than one trunk, and together they formed a dense tangle. The house, approximately eight feet from a country road, was in the midst of this tangle. It would have been almost impossible for any predator, except perhaps a snake, to capture the woodrat living in this house while the rat remained within the brush pile. There was overhead protection for approximately 10 feet in each direction from the house, and along the route to the nearby hedge row. The hedge row extending parallel to the country road did not have any houses in it. This house, one of the largest observed, was 56 inches high and 66 inches at its widest diameter; it was irregular in outline but pointed at the top. The trunks of the trees furnished support for the base while the branches supported the sides and permitted vertical growth.

There were several unusual features in this house. It had only two entrances at ground level, one on either side. One nest was a foot below the top, a second was two and one-half feet below the first, and a third was at ground level. The first nest was above the food store and in no other instance was this arrangement observed. Seemingly, the second nest was the one in use at the time the house was dismantled although the first still retained the characteristic shape. Perhaps the occupant occasionally used the first. The second nest had quantities of rabbit fur interwoven

with the shredded bark and dried grass. The third nest, located at ground level, was obviously not in use. The food store was unusual in that it contained many osage orange twigs, eight to ten inches in length, with their leaves still attached. Usually only leaves removed from twigs are brought in. In addition, there were numerous droppings scattered throughout the food store and in no other instance was such scattering observed. From observations on other houses, indications were that the woodrat removed seeds from osage orange fruit only as needed in the course of eating them, but in this house, a small store of uneaten seeds was found.

A medium-sized house dismantled on December 2, 1950, had three distinct trails leading from it. The house was on a hillside and was built around the bases of two honey-shuck trees 12 inches apart, having a low fence nailed to them. A low rock fence ran along the row of trees, but it was almost covered by leaf litter and soil washed down the hillside. These trees acted as a prop because the terrain sloped sharply at the place where they grew. For this reason, most of the house was located on the uphill side of the trees. On the uphill side, the house was 19 inches from the ground to the top, but it was 37 inches high on the downhill side. Two trails approximately four feet apart ran parallel to each other on either side of the row of trees. They could easily be followed for approximately 20 feet, but they were indistinct beyond this. The third trail coursed in the opposite direction from the others and led directly to an underground burrow among rocks. This house had three separate stores of food, each with the same kind of food. The nest chamber was in the hollow base of one of the honey-shuck trees. The entrance was three inches wide and the interior, like all others observed, had no debris or droppings within. The day following that on which the dismantling was done, the site was revisited and it was found that the woodrat, which had not been captured, had placed a few sticks and a rock over the cavity in the tree where the nest formerly was located. However, a return trip six days later revealed no further attempt at rebuilding the house. This was the only record of an attempt to rebuild a dismantled house. In most cases, if the rat does not find shelter soon, it probably falls prey to an enemy.

Objects Found in Houses

The woodrat's peculiar habit of bringing to the house any object which it is capable of carrying is well known. Woodrats in captivity immediately respond with curiosity to any inanimate object placed in the cage. Such an object is soon moved to a chosen site

in a corner or on top of the nesting material. Rocks, dung, and bones are the most common items found within houses. If an animal is killed or dies near a woodrat house, some of its bones will almost certainly be collected by the woodrat. Bones of opossums are found in houses especially frequently suggesting that often they die inside the house while using it as a refuge. Deposition of small rocks or dung on top of a house seems to represent a final stage in a period of work on the house. In many instances, an additional collection of rocks or dung can be found several inches below the surface which seemingly indicates the height of the house before the last period of repair. Numerous objects such as broken glass, cans, empty shotgun shells, and bits of paper, are commonly found in houses.

Houses in Hedge Rows

Houses built in hedge rows are usually well adapted to their immediate environment. The hedge rows provide all the necessary constituents such as cover, support, building material, food, and escape routes for supporting populations of woodrats. Hedge rows rank above all other types of house sites as far as type of support is concerned. Most of the better built and elaborate houses are found in hedge rows. Houses are permitted to undergo more vertical growth owing to the nature of support and considerably more protection from adverse weather results. Most of the houses are constructed at ground level but occasionally one is built up in a tree (Plate 9). An unused house in Greenwood County, Kansas, was built on loose boards at the edge of an old well four feet from the hedge row (Fig. 1, Pl. 10). This house was low and spreading, seemingly ineffective for protection.

In a hedge row typical of those that support woodrat colonies, 76 rods long, extending south from the south boundary of the Reservation, on a privately owned farm, there were 12 houses, all well-made and substantial, except one.

Land on the west side of the row was cultivated while that on the east side was not. After the wheat crop was harvested on the west side, there was almost no ground cover left away from the row. Coralberry grew beneath the osage orange trees of the hedge row. Ground cover on the east side was much more abundant both under the trees and away from them. It was perhaps for this reason that the bulk of each of the houses was on the east side. A wire cattle-fence 30 inches high was nailed to trees

in the row. Two strands of barbed wire had been placed above the wire fence. The top strand was approximately 40 inches from the ground. This fence aided in supporting the houses.

Presence of small stumps indicated former trimming probably to increase density of growth, but the trees had long been untrimmed and were near maximum size. The limbs arched outward and many touched the ground 10 to 12 feet from the base of the tree. In summer, it was difficult even to see a house through the dense foliage; limbs had to be cut away in order to reach a house. The dense canopy furnished excellent shelter for the houses. Coralberry added to the density of the surrounding vegetation. The tough and thorny branches provided an effective barrier in keeping cattle from grazing near the bases of the trees.

Houses at Rock Outcrops

Houses at outcrops differ in form, in structure, and sometimes in size, from those in woodland or hedge rows. Some houses are large and others consist of no more than a few sticks piled against a crevice. Even some of the larger structures do not serve precisely the same function as a house in a hedge row. Food may be stored among the sticks but an elaborate tunnel system is lacking; crevices and burrows among the rocks are used instead. The collection of sticks does serve an important purpose in preventing entrance of enemies and providing protection against adverse weather. Houses at outcrops are almost always more effectively protected from heavy rain, snow, or direct sunlight than houses elsewhere. Moreover, when trips are made away from home for feeding or breeding, an outcrop is an excellent route for traveling, with overhead protection and access to the fissures in the outcrop or spaces under boulders in the event that an enemy is encountered. Outcrops are also good avenues for woodrats migrating in search of new homes. Woodrats have tended to survive better when living at the outcrop than elsewhere. Catches were made in live-traps more consistently on the study area at the outcrop than in the woodland. In July and August, 1952, disturbance of traps at the woodland houses was occurring almost every night until by late August woodrats could no longer be trapped and most of the houses were abandoned. Whether or not they were being killed and removed from the traps by predators could not be determined, as there was never any blood, fur, or other sign on or about the traps. In this period, woodrats were being caught at the outcrop fairly consistently but in small numbers.

Traps were kept at six houses along the eastern section of outcrop for the entire period of study. Initially, more traps were used, but when they consistently failed to yield captures, they were moved to other locations. Three of the houses were on the Reservation part of the outcrop, two on the wooded part, and one on the pastureland part. Live-trapping was not done at the latter house as much as it was at the others.

A large, favorably situated house on the Reservation typical of many of those along the outcrop, had sticks almost filling the space between overhanging rock and the layer at ground level (Fig. 2, Pl. 10). The house was 85 inches long, 36 inches wide, and 19 inches high with a southwestern exposure. The part of the outcrop forming overhead cover consisted of two thick layers, the uppermost one extending 19 inches beyond the second at one place. This top layer extended 94 inches from the soil and was 10 inches in thickness. The distance from the outermost edge of this layer to the ground was 62 inches. The overhanging shelf sheltered the mid-portion of the house which tended to follow the contour of the second upper layer. The second layer was 11 inches thick midway over the house. The layer of rock upon which the house rested was 10 inches in thickness. Between it and the ground, there were numerous holes and fissures. In summer this house was in direct sunlight only in mid-morning and late afternoon. In winter it was protected from wind and blowing snow from the north. The dense thicket of dogwood which grew down the hillside in front of the outcrop furnished some protection from the south. A prairie field lay back of the outcrop. Dominant vegetation in order of estimated abundance was: white snakeroot, dogwood, fragrant sumac, plum (*Prunus americana* Marsh.), wild grape, hackberry, smooth sumac, and bittersweet. Ground in front of the outcrop and in the dogwood thicket was almost a solid carpet of white snakeroot. However, small dogwood and hackberry seedlings were numerous. A group of fragrant sumacs supported the west end of the house; two small dogwoods supported the east end. There were 17 small to medium-sized hackberry trees within 50 feet of the house. Grape and bittersweet grew back of the outcrop at the margin of the prairie field. Availability of excellent shelter and abundant preferred food caused this house to be occupied almost continually throughout the period of study, and a total of 16 woodrats were live-trapped there, including permanent occupants, nightly visitors, and others that stayed temporarily, especially when the population became low and there were other nearby empty houses. Through-

out the period of study, the house gradually deteriorated but not to the extent that some of the woodland houses did. The most noticeable change was reduction in height of the pile of sticks which increased the size of the space between the top of the house and the overhead ledge of rock. When the house was at maximum development, sticks filled the space between the upper and lower ledges of rock; however, for much of the time it remained in the condition shown in the photograph. Woodrats released after capture frequently ran directly under the upper ledge and sat on top of the house for several minutes cleaning their pelage. Others would disappear under the layer of rock at ground level. Crevices probably connected with the interior of the house.

At the same outcrop approximately 175 feet from the house discussed above, was another house also favorably situated with respect to shelter and food supply, and similar in dimensions; 84 inches long and 19 inches high. It was protected by a large overhanging ledge and many loose stones in front of the house provided escape routes. A dense thicket of grape and bittersweet grew at the edge of the outcrop above the house. A total of 15 different rats were caught in live-traps at this house.

A second type of situation for houses at the outcrop was under large slabs of rock broken away from the exposure. A live-trap was kept at a house in such a situation throughout the study period. The site was on the woodland part of the eastern section. This house was not so large as the two previously described but was maintained equally well. A total of 18 woodrats were live-trapped at this house.

When the population was reduced to a few rats in 1953, house repair was neglected in all the houses along the outcrop. The few remaining individuals tended to roam from one house to another rather than settling permanently in one house. Seemingly, repairs are made only by permanent inhabitants. Therefore, stability of numbers is important in maintenance of houses. To remain in good condition, a house needs to be permanently occupied at all times. The population is a healthy one if all houses are filled and there is competition for these houses.

Houses along the part of the outcrop in the overgrazed pasture-land were made from dead ragweed and sunflower stems owing to lack of sticks. Houses constructed of this type of material are flimsy and cannot offer as much protection to the occupant as stick houses. Woodrats building such houses probably are able to survive because of the crevices and underground burrows (Fig. 1,

Pl. 11). Perhaps if overcrowding of more suitable parts of the outcrop occurred, this part would be used more. Houses at the western section of outcrop were constructed in similar sites and were similar in form to those at the eastern section.

Houses in Rock Fences

As previously mentioned, man-made rock fences are frequently used as sites for construction of houses. Innumerable holes and crevices among the rocks provide means of escape from enemies. There are many sites available for temporary daytime retreats for migrating rats.

Two houses on the study area were located along a rock fence separating the woodland area from the pastureland. One house was made within a clump of fragrant sumac. The rock fence supported the back of the house while the sides and front were braced by the sumacs. The plants, when leafed out in summer, shaded the house for most of the day. This house was inhabited by a female rat from October, 1951, to March, 1952. After she disappeared the house was never again occupied. A second house, approximately 100 feet from this one, at the base of an old dead elm (Fig. 2, Pl. 11), was large and low. Wild grape almost completely covered the snag in summer and furnished excellent cover for the house. The rock fence and base of the snag furnished support for the back of the house. Fallen pieces of the old tree and some of the grape vines supported the sides. Seemingly, this house was used chiefly as a temporary refuge by woodrats migrating along the fence. One adult male occupied it approximately three months, but after he disappeared it was never again permanently inhabited. Another adult male caught once at this house appeared almost a month later at the outcrop and settled permanently at a house there. Principal food items in the vicinity of the two houses at the rock fence were: osage orange, dogwood, and honey-shuck. Live-stock habitually used trails on either side of the fence. This may have been a factor in discouraging construction of additional houses. Neither of the two houses were on the pastureland side of the fence perhaps as a result of the rooting of swine present there. A house was observed at a rock fence in another area built around several small box-elders (*Acer Negundo* L) growing up through the fence.

Houses in Woodland

One of the populations of woodrats on the study area occupied houses constructed in piles of brush left after small scale clearing operations (Fig. 2). Sticks in the brush heaps piled two years

before and some four years before according to the owner, interviewed in July, 1952, were mainly osage orange with smaller amounts of dogwood. The area was wooded chiefly with osage orange, honey-shuck, red elm, and dogwood. Cattle grazed on the area and weedy species such as ironweed and snow-on-the-mountain were abundant. Smooth sumac, fragrant sumac, and coralberry were common. Live-trapping operations were started here on March 29, 1952, and continued intermittently until June 20, 1954. However, most of the trapping was done in April, May, June, and August of 1952 and June and August of 1953. In early 1954, the

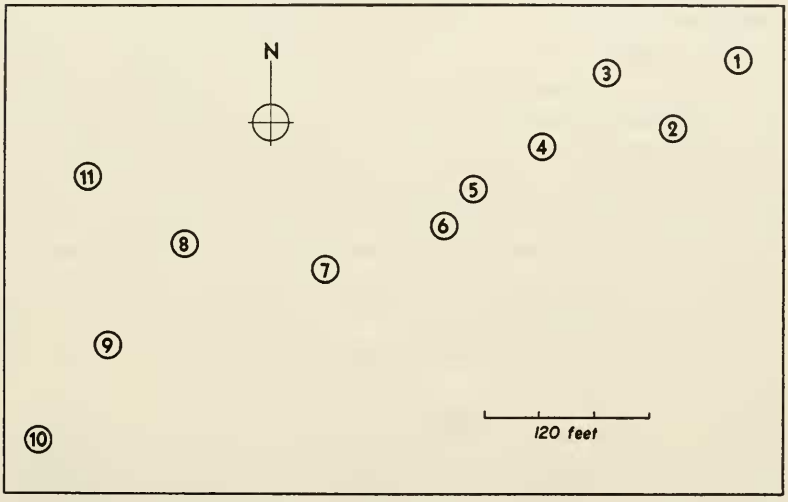


FIG. 2. Diagram of the eleven woodrat houses in the woodland part of the study area. Each of the houses, except house 11, was in a brush pile.

owner burned most of the houses and in June, 1954, the remaining houses were abandoned. When investigated in February, 1955, they were still empty and rapidly deteriorating.

There were eleven piles of brush and in each of ten of them a woodrat house was constructed; an eleventh house was at the base of an osage orange tree. Except along the nearby rock outcrop, only five additional houses (two of them unoccupied, and one built in a brush pile) were found in the entire woodland part of the study area, demonstrating strong preference for brush pile situations. The size of the population under consideration seemed to be limited by the number of brush piles as there was no sign of construction of new houses throughout the period of study. Preference for brush piles as sites for houses probably results in better support

and overhead protection for them. Dense tangles of limbs also provided additional protection from larger predators attempting to gain entrance into the houses.

The houses varied both in size and in external appearance. Some were large peaked structures whereas others were low and spreading; all were made from osage orange limbs.

House 9, a typical example, was both high and wide and possibly was the best constructed of all. Its south side faced a large open area in woods and the north side faced woodland. Surrounding vegetation included ironweed, dogwood, smooth sumac, osage orange, and one large honey-shuck tree. One limb of the honey-shuck tree offered some protection. From mid-afternoon until sundown, osage orange trees protected the house from sunlight, but the house was unshaded at mid-day. The height of the house probably compensated for lack of cover in mid-day, and, being of peaked shape, it tended to shed rain. Two smooth sumacs approximately five feet high supported the south side of the house and allowed vertical growth higher than the brush pile. Limbs of the brush pile extended away from the house in four directions for approximately 10 feet. Trails leaving the house utilized these limbs for overhead protection as far as possible. Several weed stems had been used as building material, but osage orange sticks were far more abundant.

Miscellaneous Sites

Houses of woodrats constructed inside buildings vary in size according to availability of materials. Sometimes, a woodrat is able to employ materials already present such as accumulations of boards or trash and little or no outside material is brought in. In one abandoned building a large accumulation of osage orange leaves was deposited on boards across rafters and the customary pile of sticks was absent. The nest chamber was somewhere between the walls. In other instances, large quantities of sticks are brought from the outside to construct a more typical house.

In the Flint Hills where there are steep shrubby slopes rising from small creeks, houses tend to spread downhill. A large rock or plant braces the lower end of the house and growth in height occurs at this place. One house (Fig. 1, Pl. 12) in such a situation was 110 inches long, 50 inches high at the lower end, 18 inches high at the upper end, and 74 inches wide. A few small fragrant sumacs and a limb on the ground braced the lower end. This was not completely adequate because the base was spreading some-

what downhill beyond the support. The house was approximately as high as possible and volume could increase only by spreading from the base. Another house on a comparatively level place several yards away was more typical in appearance (Fig. 2, Pl. 12). A small fragrant sumac braced the downhill side and small dogwoods supported the back. There were several houses on this slope (see pages 551 and 552); all were in an excellent state of repair. There were thickets principally of fragrant sumac, dogwood, redbud, elm, burr oak, chestnut oak, and honey-shuck. The opposing north-facing slope was not so steep and lacked the dense vegetation which resulted in preference for the south-facing slope.

Houses built along rimrock in the Flint Hills differed in appearance from those along outcrop farther east. The rimrock consisted mainly of loosely arranged boulders of varying sizes. There were no ledges and deep crevices. In one place investigated (see p. 552 and Fig. 3, Pl. 4), a rather dense but narrow thicket of dogwood grew among the rocks and the woodrats had used both plants and rocks as support for their houses. Sticks were piled between rocks at their bases, or around clumps of dogwood. Open grassland away from the rocks probably restricted woodrats to foraging only under the protective cover of the dogwood thicket.

Occupancy of Houses

Houses in favorable locations were usually occupied and visited by a succession of woodrats. The more favorable houses had histories of more continuous occupation. Occupation of houses usually reflects to some degree the condition of the population. When the population is high, a house made empty by disappearance of its owner will be reoccupied almost at once. On the other hand if numbers of woodrats are low, occupation may be slow.

The history of occupation is better known for several houses at the eastern section of outcrop than for those on the other two areas. The reason for this is that traps were kept at these houses throughout the study. The history of three of these will be presented as examples of succession of occupancy. Population trends are also reflected in these histories.

(1.) This house was occupied by an adult female in March, 1951. In May, an adult male took over and the female was forced to find another house. The male stayed until July. The house remained unoccupied through August but was inhabited by another adult male in September, and he remained until his disappearance in January, 1952. The population was low at this time

and the house remained empty through February. In March, another adult male took possession and one subadult female visited the male. No live-trapping was done there in April, May, and June, 1952. In July, a new adult male was living in the house and he remained there until late November. Two nights of trapping in December did not result in a capture at this house, and seemingly it was empty through February and March, 1953. In May, an adult male was caught once but never seen again. The population by this time was extremely low and the few remaining rats, both males and females, were moving from house to house. It became almost impossible to establish ownership of houses. An adult male was caught here one time in June, but seemingly a subadult female "owned" it and was alternating between this one and another nearby house from June until she disappeared in mid-August. When trapping was resumed on September 6, an adult male had occupied the house and was still present on November 7. However, he moved and the house remained empty in December and January, 1954. Trapping was not resumed at this site until June, 1954, and a subadult male was then living there. It is of interest to note that this house was most commonly inhabited by males.

(2.) An adult female was living in this house in March, 1951. She maintained occupancy until her last capture on July 7, 1951. An adult male visited her in April and again in May. A juvenal female, presumably the offspring of the adult female, was caught in June. The young female disappeared in early July. No trapping was done in August, and in September, a juvenal male was caught there just once. In October, the house was occupied by another young male from another part of the outcrop. He remained until early December and was replaced by a larger male. The latter male disappeared in January, 1952. The house was not occupied in February and March. When trapping was resumed in July, a subadult female was living in the house and she remained until late November. She was visited by an adult male in July. The house was empty in December, 1952. In February, 1953, a subadult female was caught once but was never seen again. After this, the house seemingly was not permanently occupied although several rats were caught at this site. However, none of them was repeatedly recaptured. An adult male was live-trapped one time in each of the months of May, June, and September. Also in September, another adult male, and two subadult females, were live-trapped at this house; the male was again captured in November.

(3.) A subadult male was caught just once here on March 31, 1951, but he was never seen again. In April, the house was taken over by an adult female and she remained until the last capture on October 21, 1951. An adult male visitor was captured twice in April and three times in May. A subadult male visitor was captured here once in December, a different subadult male in February, 1952, and a young adult female in March. When trapping was resumed again in July an adult female that had been living at a nearby house was caught one time. Two juveniles, a male and a female, were caught here in July. Possibly the adult female had been living here previous to July, and after the young were weaned, she moved to the nearby house. Both young disappeared by the end of July. On September 8, a subadult female was found in a live-trap at this house but she disappeared and two days later a young male took possession and remained until November 22. He was seemingly forced out or captured by an enemy because a subadult female was caught on November 23. She was still living in the house in December. An adult male was captured once in November and once in December. The female seemingly stayed through January, February, March, and April. In May, a young female, probably the offspring of the female mentioned above was caught. She moved the first of June and the mother was again captured here in August. During the last half of 1953, the house was not permanently occupied by one individual. A subadult female was trapped here once in November and again in December. An adult male was captured once in December. The house was empty in January, 1954, and when trapping was resumed again in June, 1954, a subadult male was taken. The house was dismantled in February, 1955, and found to be unoccupied.

Food Habits

Food items studied were mostly those found inside dismantled houses. Woodrats released from live-traps were observed on several occasions to eat certain plants. Their natural diet is composed largely of plant material although flesh, both cooked and uncooked has been eaten by rats in captivity.

Food habits of this species have not been studied in any detail. In Florida, Pearson (1952:460) fed several native plants to captive *N. f. floridana* noting acceptance or refusal of each. These captive animals had access to a constant supply of corn and sunflower seeds; therefore Pearson's results may not reflect the preferences of the animal under natural condition. In Alabama, Howell (1921:52-53) found that *N. f. floridana* was eating hickory nuts and papaw seeds.

Bailey (1905:110) found that *N. f. attwateri* in Texas was eating nuts and leaves of the walnut tree, cactus capsules and stems, acorns, juniper berries, wild grapes, blackhaw, mushrooms, and Mexican buckeyes. Also in Texas, Strecker (1929:220) found that woodrats ate pecans in great numbers.

This species of woodrat demonstrates great adaptability in its feeding habits and ability to thrive on almost any kind of plant material that is available. The type of food therefore is usually not a limiting factor. Quantity is basically more important than kinds. If a house is suitably located, the woodrat is able to subsist on most any kind of plant material in the vicinity as long as it is present in sufficient quantity for storage purposes.

The drive that compels woodrats to store food in quantity usually does not commence until in September or October. In 1951, the first sign that storing had begun was noted at a house occupied by an adult female on September 22. She had collected numerous dogwood leaves and six honey-shuck "beans". On October 7, 1951, a large number of white snake-root leaves, some loose and some attached to stems, had been brought to another house occupied by a young male. Both of the houses were at the outcrop. In each case the leaves were green but were becoming brittle. In 1952, signs of active food gathering were first noted on October 17. An adult male living in a house at the outcrop had brought in dogwood twigs, goldenrod plants, part of a compass-plant, and several bittersweet fruit, none of which had been noted one week previously.

Woodrats in this area do not store much food in spring and summer. Several occupied houses opened in July, 1952, were found to have little food within. One had a few osage orange and ironweed leaves; another had only a few osage orange leaves; two were completely empty; and the fourth had one ironweed plant and part of an old ear of corn.

Woodrats will often store more food than they can consume in winter and a substantial amount will be left when storing begins anew. On April 7, 1951, several empty bittersweet capsules were noted to have been carried to the outside from two houses at the outcrop. As bittersweet does not begin to flower until May, this must have been food stored the previous autumn. Several houses dismantled in early winter contained small quantities of osage orange leaves remaining from stores of the previous year. Leaves stored in autumn will remain green until the following spring but not until the following autumn. Seemingly, if the food store is depleted in winter, food will be collected and stored in early spring.

A house dismantled on June 12, 1952, contained a cache of fresh dogwood leaves. Several opened honey-shuck "beans" were found but no other usable food. The appearance of the dogwood leaves indicated they had been recently collected probably from a small dogwood plant growing up through one side of the house. In summer, woodrats probably do most of their feeding while foraging but frequently bring small amounts to the house for daytime feeding.

The urge to store food dominates all other activities once the drive has begun. Observations on captive woodrats indicate that in nature they would be highly vulnerable to predation during this period. Specimens kept in outdoor cages were regularly fed sunflower seeds placed in a small metal cup wired to the cage. In summer they were content to feed directly from the cups. However, a rather rapid change in behavior occurred with the advent of autumn. The seeds were removed from the cups by the woodrats and placed in a pile in one corner of the cage. Owing to the fact that the cages were provided with wire bottoms many of the seeds fell through to the ground. One female persisted in losing almost all of her food this way at each feeding. The seeds were at first removed from the cups only after the observer had left the vicinity of the cages, but soon the rats commenced removing them even before filling the cup was completed. The rats seemed oblivious to the presence of the observer. The food finally had to be changed to commercial dog biscuits large enough so that they would not fall through the bottoms of the cages. From these observations on animals born and reared in captivity, it seems that storing behavior is instinctive and not learned.

For the kinds of plants eaten in eastern Kansas see Table 5. Leaves and seeds of the osage orange tree comprised the bulk of the food store more often than all of the other foods combined. This is because the osage orange is abundant in hedge rows and woodland, and is highly preferred as a house site. Probably cover is a more critical factor than food in determining the choice of osage orange as a house site. Danger to the foraging rats from enemies is considerably reduced because the distance that the rat is required to go for food is only a few feet from the house or from a suitable escape route. The osage orange tree is extremely hardy and considerably more resistant to drouth than most other species of plants of this area. Osage orange trees produce prodigious crops of fruit; each fruit contains hundred of seeds. After falling, the fruits are slow to deteriorate but turn brown upon freezing. Of the vertebrate species living in this area, only the

woodrat and squirrel use the fruit as food to any great extent, however, abundance overcomes any possibility of serious interspecific competition.

Both entire fruits and pieces are carried to the house. The fleshy seed coat usually is removed to the outside of the house and is discarded; only the seed is eaten. In every instance observed the stored fruit was accompanied by an equally large amount of leaves.

Table 5. Parts of the Plant Foods Which Were Utilized and the Place Where Each Observation Was Recorded. Often Woodrats Seek Food Immediately After Release from a Live-trap; Numerous Observations Were Recorded in This Manner.

Plants	Parts eaten				Where recorded	
	Leaf	Fruit	Seed	Stem	Food store	Sight record
Common Ragweed (*Ambrosia artemisiifolia*)	X					X
Bittersweet (*Celastrus scandens*)	X	X	X		X	
Hackberry (*Celtis occidentalis*)	X	X	X		X	X
Lamb's-quarters (*Chenopodium album*)	X			X	X	
Thistle (*Cirsium undulatum*)	X				X	
Dogwood (*Cornus Drummondi*)	X	X	X		X	X
Red Haw (*Crataegus mollis*)		X			X	
Honey-Shuck (*Gleditsia triacanthos*)	X		X		X	
Coffee Tree (*Gymnocladus dioica*)			X		X	
Black Walnut (*Juglans nigra*)			X		X	
Osage Orange Tree (*Maclura pomifera*)	X		X		X	
Climbing False Buckwheat (*Polygonum scandens*)	X				X	
Wild Plum (*Prunus americana*)		X	X		X	
Burr Oak (*Quercus macrocarpa*)			X		X	
Chestnut Oak (*Q. Muehlenbergii*)			X		X	
Fragrant Sumac (*Rhus aromatica*)	X					X
Smooth Sumac (*Rhus glabra*)	X		X		X	
Poison Ivy (*Rhus radicans*)	X		X			X
Poison Oak (*Rhus Toxicodendron*)		X			X	
Gooseberry (*Ribes missouriense*)		X			X	
Compass-plant (*Silphium laciniatum*)	X				X	
Greenbriar (*Smilax tamnoides*)	X	X			X	
Horse-nettle (*Solanum carolinense*)		X			X	
Black Nightshade (*Solanum nigrum*)		X			X	
Goldenrod (*Solidago* sp.)	X				X	
Milo (*Sorghum* sp.)			X		X	
Coralberry (*Symphoricarpos orbiculatus*)	X	X			X	X
Wheat (*Triticum aestivum*)			X		X	
Grass (unidentified)	X		X		X	
Ironweed (*Vernonia Baldwini*)	X				X	X
Winter Grape (*Vitis vulpina*)	X	X			X	X
Corn (*Zea Mays*)			X		X	

Even though some individuals exhibited preference for the fruit, the leaves were preferred as a general rule. Leaves lose most of their water content and become brittle rather quickly. They are stored in a tight compact bundle, and the rat feeds while on a platform beside the food store. Occasionally, small amounts of food are eaten at the nest chamber as indicated by discarded pieces around the opening. In every case observed, the food store, if in a stick house, was placed in the upper part while the nest chamber, situated closer to the base, had added protection from inclement weather.

In several kinds of plants for example, wild plum, both fruit and seed are eaten. Probably the same is true of most seeds enclosed by a fleshy fruit. The fruits of climbing bittersweet and grape are widely sought after, but their occurrence is sporadic and they are important only under local conditions. The large "beans" of honeyshuck trees are abundant near some houses on the study area, yet they are not used to the extent that their abundance might indicate.

Goldenrod, ironweed, compass-plant, fragrant sumac, and lamb's-quarters and especially ragweed, seem to be unpalatable and are only occasionally utilized. Even though they may be locally abundant, usually only a single plant or a few leaves are found and they have never constituted the bulk of a food store.

Woodrats were found living where oak trees were common only in the Flint Hills. From the number of opened acorns around several houses in Riley and Marshall counties, I concluded that these woodrats rely heavily on oak mast. Small berries such as those from poison oak, dogwood, and wild grape are most often brought to the house in clusters instead of individually. One house yielded approximately one-third of a bushel of poison oak berries.

A few blades of grass in a food store near the abandoned quarry on the Reservation constitute my only record of this woodrat utilizing native grass. Vorhies and Taylor (1940:513) noted similar scarcity of grass in the diet of *N. albigula* in Arizona. However, Murphy (1952:210) thought that the early summer diet of *N. f. osagensis* in Oklahoma was mainly grass.

There are reports of other species occasionally feeding on insects (Linsdale and Tevis, 1951:296 and Vorhies and Taylor, *op. cit.*: 501). The wings, parts of the head, and the thorax of a cicada found on the feeding platform of a house dismantled in November, 1953, constitute my only evidence of a woodrat feeding on animal matter. Vorhies and Taylor (*loc. cit.*) found that cicadas consti-

tuted over half of the total percentage of animal matter in the diet of the white-throated woodrat in Arizona. Murphy (*loc. cit.*) found animal remains (scorpion, snail, and grasshopper) in three of several stomachs he examined.

Food preferences are not clear-cut for this animal. The favorite food of one population may not be used at all by a population in another locale. Woodrats that construct houses at or near osage orange trees usually eat leaves and fruit of this tree instead of any other plants that are available, but exceptions have been noted. A case of unusual selectiveness by the occupant of a house was observed in Greenwood County in July, 1954. The house, situated in a hedge row, was dismantled and found to contain a large store of honey-shuck "beans." This food even though it may be abundant is usually not preferred if products of osage orange trees are readily available. The food store of another house that was built at the base of an osage orange tree in a hedge row consisted entirely of the spikelets of wheat which was growing adjacent to the row. On another occasion, a dismantled house contained large amounts of milo which was growing in an adjacent field. In no instance was there any evidence that woodrats were significantly damaging cultivated crops. In some instances woodrats become pests when living in the vicinity of human dwellings by removing stored products such as fruit and nuts.

One large house contained approximately one bushel of osage orange leaves, some attached to twigs, and approximately 30 "hedge balls."

On July 23, 1952, a male when released from a live-trap went directly to a ragweed plant and ate one leaf. Then he investigated a dogwood seedling, a coralberry plant, and a white snake-root plant without eating any of them. This was the only instance in which ragweed was known to have been eaten even though it was abundant in the vicinity of several houses.

Seemingly, woodrats need green plant material for nutritional purposes other than water content. An adult male kept for four days in captivity was provided water which he frequently drank. Sunflower seeds and chick scratch were provided. When released at his house, he almost at once began foraging several feet from the house even though it was daytime. A rabbit that had been utilizing the house as shelter ran out and stopped approximately 10 feet from the house. The woodrat advanced to within two feet of the rabbit, paused to eat small berries fallen from dogwood trees

and, seeming to be completely oblivious of the rabbit, clipped a small dogwood seedling approximately 15 feet from the house, stuffed it into his mouth, and ran back to the house.

Woodrats also exhibit preference among plants of the same kind. A female released from a live-trap on May 20, 1951, went directly to a dogwood seedling six inches in height. Similar plants were abundant around the trap. She smelled the plant but took another one a few inches away. Similar selective behavior has been observed several times in rats which rejected one plant and took another that was not appreciably different to the observer.

Usually a woodrat obtains its food within a few yards of the house. Accessibility of desired food items is one of the most important factors in determining whether or not a house is continually occupied by a succession of woodrats, over a long period of time. One house at the outcrop was in a good location and well protected by a large over-hanging shelf of rock. When found soon after the beginning of my study, the house was obviously not new judging from its large size and amount of litter around entrances. Approximately 30 feet along the outcrop from this house and 15 feet down the hillside, there was a small thicket of wild plum. Although the crop was poor in the dry years of 1952, 1953, and 1954, woodrats had previously relied heavily on this fruit as food, and there were large quantities of opened pits around the above house. In addition, a large wild grape vine grew at the outcrop at one end of the house and there were several bittersweet vines within a few feet. The excellent location and the proximity of highly preferred food items undoubtedly contributed to the success of this house.

Considerable distance is occasionally traversed in order to obtain a desired food item. At one house the minimum distance traveled to obtain corn was 150 feet.

Woodrats have often been observed carrying food material to their houses after they were released from live-traps. Usually, if a weed was the desired item, the rat quickly cut the stem a few inches from the ground. The rat sometimes stood on its hind legs and clipped off the top portion. With the aid of the front feet, the plant was grasped securely in its mouth, and with its head thrown back, the rat carried the food item back to the house. Another procedure when gathering foliage is to fold the material into a more compact bundle by adroit manipulation with the front feet and mouth. When the bundle is of sufficiently small size, it is grasped in the mouth and carried into the house.

Captive woodrats used the front feet and nose to compact the food into the store pile. Small objects such as seeds or small berries are carried several at a time by filling the mouth to capacity. When the rat is eating, it holds the food in the front feet, taking small bites and chewing rapidly. While eating, the woodrat is remarkably dextrous with the front feet, holding the food firmly by appressing the four toes against the palm in much the same manner as a human would grasp an object if he lacked the opposable thumb. The food is held with both forefeet or only one and can be turned to any desired position with no difficulty. While eating, the woodrat maintains a sort of half-crouched position resting on the hind legs and using the tail as a prop.

Occasionally in the course of gathering food, a woodrat may stop for short periods to feed while away from home. Vestal (1938:27) found that *Neotoma fuscipes annectens* Elliot, in California feeds away from the house at night. Observations made on a female and her two young at night with the aid of a red light indicated that each animal alternated in periods of active foraging, eating from the food store, and resting in the nest which was in a building where it could be readily observed. Periods of feeding at the food store lasted up to ten minutes and were sometimes repeated within an hour.

In no instance did I find that woodrats had caused pronounced damage to surrounding vegetation such as the girdling of shrubs and small trees by rabbits and meadow voles. Along the outcrop on the study area, the spread of the hackberry tree is probably retarded to a slight degree by woodrats clipping shoots less than one year old. Conversely, in other situations, woodrats may actually aid in plant propagation by serving to spread seeds to more favorable locations. Dickens (1928:7) in discussing the forest situation in Kansas, attributes new generations of hardwood trees such as oaks and walnuts, to squirrels and woodrats, in that acorns or walnuts, forgotten or neglected, crack by winter freezing and sprout in spring. However, in most instances, the effect of man and domesticated animals upon vegetation overrides and masks any effect attributed to woodrats.

More subtle changes caused by woodrats which are difficult to detect and interpret do occur and influence community activity to some extent. Smooth sumac commonly grows around the margin of woodrat houses and sometimes up through a portion of the house or even surrounds the house with a small thicket. Probably these plants grow from uneaten seeds brought in by the wood-

rat as food and discarded along with other debris. This increase in plant cover furnishes temporary shelter for other species of vertebrates such as the cottontail. Increased humus resulting from discarded parts of food items and also by falling leaves of surrounding plants, attracts seed-eating and insect-eating birds. Reptiles including small snakes and box turtles sometimes seek shelter in the tangles around woodrat houses.

Probably the white-footed mouse, *P. leucopus*, is the most important competitor for food especially along outcrops which provide favorable habitat for the mouse. This mouse is a seed eater and stores quantities of food (Allen, 1938:406; Burt, 1940:23). It was the most numerous vertebrate cohabitant of the woodrat along parts of the outcrop on the study area. Besides competing with the wood rat in gathering food it probably actually steals from the food stores, because it commonly uses houses of the woodrat as shelter. If present in larger numbers, it could have detrimental effects on woodrats which under local conditions rely on foods (seeds, nuts, etc.) other than leafy parts.

Competition between individual woodrats is probably most intense among animals occupying outcrops when such foods as bittersweet or grape, which ordinarily are not abundant, are preferred food items. Weaker individuals can subsist on other foods and it is not likely that permanent harm to the colony would occur. Only in the case of an extreme shortage of food would intraspecific competition for food be serious. Such competition has not been observed. Availability of house sites, and psychological traits associated with special relationships seem more important than competition for food in determining population size.

Behavior

Temperament and Sociability

Captive woodrats are generally hostile in their demeanor toward humans. Individuals may become more mild tempered after a lengthy period of confinement, but they always remain unpredictable. Murphy (1952:209) noted similar behavior for *N. f. osagensis* in Oklahoma. Attempts to tame woodrats reared from birth in captivity have been unsuccessful. Captives have been induced to take food from the fingers as it was offered to them through the wire of the cage. However, occasionally they would attempt to bite. One month elapsed before a captive subadult male would accept food from the hand of the observer without attempting to bite.

A captive juvenal female weighing 64 grams and estimated to be four to five weeks of age attempted to bite when I placed food in the cage. After three months she had become even more contentious and although humans were about almost constantly, she never exhibited any degree of tameness throughout the year of her captivity. Her aggressiveness was more apparent than that of the male.

Individuals of both sexes handled in the field varied in temperament from extreme passiveness to extreme viciousness. Some offered little resistance to being handled; others struggled until they were nearly exhausted. Such a rat resisted handling by rapid defecation, urination, squealing, and clawing with the hind feet. Any object within reach of the mouth was grasped and chewed vigorously. On several occasions the rats handled have fought so energetically that when released, they were too exhausted to seek shelter immediately. Other individuals seem to enjoy being handled.

Male woodrats are usually antagonistic toward other males. When the cages of two, one much the larger, were placed together, the smaller more aggressive one immediately sprang against the wall of his cage attempting to reach the larger male. Both would lunge at each other clawing viciously at the wire separating them. When both were placed in the same cage, they slowly approached, touched noses and began fighting. The smaller gained the advantage momentarily, attempting to bite the other's neck. While fighting, both squealed loudly. Several times both would rear up on the hind legs and weave back and forth. During pauses they stared intently at one another chattering their teeth. In a fighting stance commonly assumed, the rat rested on the hind legs, while biting, and while lashing with the front feet. This latter action probably produces the tears so frequently observed in the ears. Practically all old adult males have several tears in one or both ears. A few old large males had the margins of the pinnae so torn as to appear scalloped. Young males before their first season of breeding rarely have torn pinnae. Small scars or wounds on the muzzle, lips, feet, and tail are probably inflicted by claws when the rats are fighting.

When the smaller of the two males was placed in one compartment of a double wire-cage separated by a sliding door from an adult female he exhibited the same belligerence and persisted in attempting to attack, until he finally gained entrance to the female's compartment in the night and killed her.

Hamilton's (1953:182) and Pearson's (1952:463) accounts suggest that the subspecies, *N. f. floridana,* may be more mild tempered toward their own kind than this subspecies. Pearson (*loc. cit.*)

described two adults and six young living together in harmony. Hamilton (*loc. cit.*) mentions conflicts between individuals but such hostility was of short duration.

Communication

Vocal sounds are rarely made except when in distress. A woodrat being handled frequently emits a succession of high pitched squeals each of which may be of three or four seconds duration. On several occasions, a soft plaintive whine varying in pitch has been heard coming from a house. When the ear or toe is clipped a woodrat often emits a short, sharp, "scream." New born young are capable of emitting scarcely audible, high pitched "peeps." Woodrats that are fighting usually squeal loudly.

The most characteristic sound produced by this woodrat is thumping of the hind feet, a reaction that is developed early in life. The rate and intensity of the thumping varies individually and also according to the degree of disturbance. Both feet or only one may be used in producing this sound. When greatly disturbed, rats have been observed to raise the entire rear part of the body from the substratum and stamp the feet forcibly. Seemingly this thumping is a reflex and not a voluntary means of communication as suggested by Vorhies and Taylor for the white-throated woodrat (1940:471). It seems to serve chiefly as a warning evoked by fear or anger, comparable to the behavior of a rattlesnake vibrating its tail. A male woodrat usually begins thumping when it meets another male. The posture, facial expression, and ruffled fur between the shoulders are all indicative of anger. On the other hand, thumping that usually commences when an investigator approaches a rat in a live-trap suggests a fear reaction. Rats usually withdraw into the nest box as far as possible and curl up with the head hidden. In still other instances, the behaviorism suggests that the rat is merely annoyed, as when a captive, engaged in an activity such as feeding or arranging the nest, thumps at a person approaching the cage but without stopping its activity.

Rattling of the tail, highly developed in the dusky-footed woodrat (Linsdale and Tevis, 1951:234-240 and Vestal, 1938:3-6), has been heard only once in the present study. A male caught on July 15, 1952, dashed out of the nest box into the wire trap as I approached. In addition to thumping the hind feet, he vigorously vibrated his tail on the bottom of the cage. Preceding combat with another male, one sharply struck the bottom of the cage with the tail several times but it did not vibrate the tail.

Development of Senses

Although hearing is acute, this woodrat seemingly is unable to recognize certain sounds indicative of possible danger. The cry of a nearby red-tailed hawk, heard several times as a woodrat was released from a live-trap, elicited no response. Sudden nearby noises such as rustling of leaves or sticks will cause a woodrat to be on the alert instantly. Abrupt noises to which captive woodrats are unaccustomed cause them to jump.

Lindale and Tevis have suggested (*op. cit.*:255) that the eye of a woodrat is adapted to arrhythmic activity rather than strictly diurnal or nocturnal activity. On many occasions, woodrats released in broad daylight proceeded directly to the nearest shelter even though such shelter was several feet away. Repeated observance of this reaction has led to the conclusion that sight must be well-developed in order for them to travel so rapidly over such a direct route. If an observer moves slowly synchronizing his movements with those of a woodrat, it is not able to detect his presence. However, the woodrat instantly perceives any sudden movement if the rat itself is motionless. At night a woodrat may rely more on other senses such as touch or smell when it is active.

Woodrats both in captivity and in nature have been observed many times smelling various objects or "testing" the air. Strange food given to a captive woodrat is always smelled before being eaten. The tip of the nose and vibrissae oscillate rapidly when smelling. Seemingly, the sense of smell is well-developed and is useful in choosing food, recognizing other woodrats, and possibly detecting enemies.

Tactile sense is especially well-developed in this animal. Seemingly touch is most acute on the vibrissae, of which, the longest extend beyond the width of the body. Tactile response is also elicited when various other parts of the body are touched. If a rat's abdomen is touched while the animal is being held, the rear feet are brought up and tightly appressed against the abdomen. The hairs on the margin of the pinnae are especially sensitive. Usually the ear is instantly moved and frequently the entire head is jerked around toward the source of stimulus. Blowing on the face is irritating to most rats and they usually react by moving away.

In captivity extremely bitter foods such as cranberries were eaten eagerly even though the rats were not suffering from hunger. Woodrats are generally attracted by sweet foods; however, salt was eagerly licked from a soda cracker by a male in captivity.

Sanitation

This woodrat is sanitary in its habits. Captive animals always choose a particular site, usually a corner of the cage, for defecating and urinating. Feces are rarely found scattered about in the stick houses. There are usually one or more sites where the occupant habitually defecates. Along outcrops droppings are easily detected and have never been observed scattered randomly.

Care of Pelage

Woodrats give much attention to their pelage. When the underparts are being cleaned, the woodrat rests on the hind legs and the base of the tail. The fur is licked vigorously and the front feet are used to part the hairs for more efficient cleaning. As the skin is loose, the front feet are used to pull areas that are not readily accessible within reach of the mouth. The characteristic procedure in cleaning the face is to lick the front feet and rub them over the head in a circular movement. A young woodrat only 15 days old was observed cleaning its face with the characteristic circular movements of the front feet. Its movements were awkward and it lost its balance and fell forward. The tail is cleaned as rigorously as are other parts of the body. It is grasped with the front feet and turned from side to side while being cleaned. After defecating, captives have frequently been observed to bend, with the head between the rear legs, and clean the anal area.

An adult female observed on June 18, 1952, dusting at a small sandy spot three feet from her house, rolled on her back and left side, vigorously wriggling in the sand. After pausing a few seconds to clean her face, she repeated the procedure before returning to the house. This was the only instance recorded of dust bathing, but dusting spots that evidently were used similarly have been observed near many houses. Probably dusting is usually done at night.

INTERSPECIFIC ASSOCIATIONS

General Considerations

The relation of the woodrat to other animals of its environment may be broadly divided into commensalism, parasitism, predation, and competition. Competition may involve either food or space. Some associations are intimate and of great importance whereas others are casual. Intimate associations are exemplified by a rattlesnake living at an outcrop inhabited by woodrats and preying on them, or by fleas living on the rat. Birds foraging around a wood-

rat house or skinks seeking temporary shelter in it provide examples of casual associations.

Associates are arranged systematically as parasites, predators, and commensals. When a species fits more than one of these categories it is discussed from both standpoints but listed in the category where it is believed to exert the greatest influences.

Parasites

Several specimens from various localities were critically examined for helminths but none was found. Murphy (1952:213-216) found five kinds of helminth parasites, three nematodes (*Longistriata neotoma* n. sp., *Bohmiella wilsoni*, *Trichuris muris*), and two cestodes (*Andrya* sp. and *Taenia taeniaeformis* larvae) in 50 woodrats (*N. f. osagensis*) examined from Payne County, Oklahoma. He stated that previously only a single species of internal parasites had been reported from this species of woodrat. Most of the woodrats handled in my own study were those on the area where intensive population studies were being made, and they could not be sacrificed. Much more information was obtained concerning external parasites, because they can be in most cases easily observed and collected even on a live animal. In the course of study, one species of tick, three species of fleas, 12 species of chiggers, and one dipteran fly were found parasitizing woodrats. Only the chiggers were found in heavy infestations, and there was never any indication that infestations were fatal.

Warbles

A male woodrat live-trapped on the study area on May 20, 1951, had a large warble on the underside of his neck. This was the first time this parasite was observed on woodrats of the study area even though Dr. Henry S. Fitch had been trapping woodrats on the Reservation since 1948. In 1951, only two other instances of warble infestation were recorded, one in September and one in November. On July 12, 1952, an adult male with a large warble on the throat was live-trapped. The animal was brought to the laboratory and placed in a cage set over a tray of loose soil. On July 19, 1952, the larva was found to have emerged. It was placed in a glass jar containing sand. Approximately two weeks later the adult fly had emerged and was found dead. Several other attempts to obtain adults failed. The fly was identified as *Cuterebra beameri* Hall, by Dr. Curtis W. Sabrosky. This fly was described as new from adults reared from warbles that had emerged from woodrats (*N. f. osagensis*) collected in Greenwood County, Kansas

(Hall, 1943:25-26). Beamer, Penner, and Hibbard (1949:49) found that the eggs of this fly were laid at random around the entrances of the woodrat houses; infestation occurred when the woodrat came into contact with an egg, which stuck to the fur. They observed that captive females each laid approximately 285 eggs.

Of the 105 woodrats live-trapped, 17 (16.2 per cent) were recorded as infested with warbles. Beamer, Penner, and Hibbard (*op. cit.*:47 and 50) collected 72 woodrats from Greenwood County and 13 per cent were infested. Linsdale and Tevis (1951:163) found 94 or 43.5 per cent of 216 *N. fuscipes* live-trapped were infested. Vorhies and Taylor (1940:509) found eight per cent of 275 *N. albigula* examined in Arizona infested. Murphy (1952: 216) found eight per cent (4 of 50) of the *N. floridana* that he examined in Oklahoma to be infested. Linsdale and Tevis (*loc. cit.*) examined the 216 woodrats 2,213 times and recorded an eight per cent infestation. In this report, the 105 woodrats were examined 660 times and warbles recorded 31 times or 4.6 per cent of the time. Woodrats collected by me in other parts of eastern Kansas were seldom found with warbles.

In one infestation, four warbles were present, but in every other instance there was only a single warble. In one instance, an adult male became infested twice in the same season. On August 18, 1952, a large warble was observed on his chest. The rat was again caught three days later and the warble was removed. On October 18, 1952, another small warble having an entrance hole measuring one millimeter in diameter, was observed on the underside of the lower jaw 20 millimeters from the mouth. One week later the swelling was 20 millimeters high, the hole was three millimeters in diameter, and the larva seemed nearly ready to emerge. No sign of its presence was detected when the woodrat was caught one month later.

Of the woodrats infested, 71 per cent had the warbles on the throat, which also was the most common site of infestation reported by Vorhies and Taylor (*op. cit.*:508) and by Linsdale and Tevis (*op. cit.*:167). The other sites of infestation observed were: behind the ear; on the underside of the jaw; on the chest between the front legs; on the front legs; on the belly; and immediately below the eye. An adult male live-trapped November 11, 1951, had a hole 12 mm in greatest diameter on the left side of his face, where a warble had emerged. The hole was only five millimeters from the eye, which was almost closed by swelling; vision probably was im-

paired. The center of the hole contained dried black substance. When the rat was recaptured 21 days later no visible sign of the warble or its effects remained.

Of the numerous *Peromyscus leucopus* live-trapped on the study area none was found to have warbles even though many were living in or near woodrat houses. *C. beameri* may be host specific for this woodrat. Warbles were observed in May, June, July, August, September, October, and November. The peak of infestation occurs in July and August. More warbles were recorded in 1952 than in 1951, 1953, and 1954 combined. The April-September period of 1952 was the driest on record. The 1952 precipitation for the Lawrence area was 11.60 inches below average. In 1951 precipitation was 15.28 inches above average and only three woodrats were recorded with warbles. These data seem to indicate that warble infestations are more prevalent in periods of dry weather. Of the woodrats infested, seven were adults, six were subadults, and four were juveniles. More females (11) than males (6) had warbles.

The warble fits the description of Linsdale and Tevis. Hair was always missing around the site of the warble and seemingly this is not because of scratching but is caused by the parasite. The warble in nearly every case observed pulsated and exuded a dark sticky liquid. On June 2, 1953, a female that was caught had a warble on her throat. The hole was only one millimeter wide, but there was already a bare spot around the hole 16 millimeters in diameter. The hair begins to fall soon after the warble enters. A warble in the neck of an adult male, and near time of emergence was extracted with considerable effort by grasping it with a pair of heavy blunt forceps and exerting a steady pull. This extraction did not seem to be painful to the woodrat. The hole left was seven millimeters in diameter. The warble was 24 millimeters long and 13 millimeters wide when expanded. Another warble removed from a female August 15, 1953, measured 30 millimeters long and 13 millimeters wide, and the hole it left was eight millimeters in diameter. In this instance also there seemed to be no pain associated with the removal of the warble. The sides of the hole left by the warble soon dry and harden with a black scabby surface. The wound heals rapidly and hair grows back so that within a few days there is no visible sign that the woodrat had carried a warble. For the most part, the woodrat and this parasite are well-adjusted. Nevertheless, an adult female having a large warble on the throat obviously near time of emergence when she was live-trapped on September 23, 1951, died in captivity on October 5. The decayed remains of the

parasite were found in the cavity and the adjacent flesh was yellowish and moist indicating an infection. This rat was carefully autopsied but no other possible causes of death could be found.

Fleas

Three kinds of fleas were found on woodrats: the histrichopsyllids *Conorhinopsylla nidicola* Jellison and *Epitedia wenmanni* (Rothchild) and the dolichopsyllid *Orchopeas sexdentatus* Baker.

More males than females were found with fleas. This is possibly a result of a greater wandering tendency among the males. Fleas were observed on woodrats in every month, but were noted more commonly in May, June, July, August, September, and October. Fewer cases of flea infestation were observed in the wet year of 1951 than in the dry year of 1952. In May, 1952, live-trapped woodrats of all age classes were noted to be more heavily infested with fleas than those taken in the same month of the previous year. This trend continued for the remainder of 1952 (Table 6), and into 1953.

The species *C. nidicola* was described as new from specimens taken from woodrat nests six miles north of Lawrence, Kansas (Jellison, 1945:109). A fourth flea, *Epitedia neotomae,* described as new in 1946 was collected from woodrat nests five miles north of Lawrence and was also taken at the type locality from a spotted skunk, *Spilogale putorius* (Linnaeus), (Jameson, 1946:62-64). However, this flea was not found in my study.

Most of the rats live-trapped on the study area were infested with *O. sexdentatus,* and *C. nidicola* was found there only once. However, in nest material from houses dismantled approximately one mile from the study area, all three kinds were found. One nest contained 100 per cent *C. nidicola.* Another contained 95 per cent *C. nidicola,* four per cent *E. wenmanni,* and one per cent *O. sexdentatus.* There were many fleas in the nest and hundreds of flea larvae. A female rat caught in a snap-trap from one of the houses had six *E. wenmanni* and three *C. nidicola* on her when examined. The procedure to obtain fleas from dead woodrats was to place the animal in a plastic bag along with some paradichlorobenzene crystals as soon as it was removed from the trap. In this manner fleas would be killed, drop off the host, and could easily be found in the bottom of the sack.

It seems that the different kinds of fleas have different preferences in the times chosen to attack the host. *C. nidicola* seemingly prefers to feed by day while the woodrat is in the nest and is not regularly carried about when the host leaves the house, but

O. sexdentatus stays on the rat and is not regularly found in the nest. Possibly different kinds of fleas are dominant in different locales.

Table 6. A Comparison of Flea Infestation Between the Wet Year of 1951 and the Drought Year of 1952.

Month	Number infested		Number live-trapped		Per cent infested	
	1951	1952	1951	1952	1951	1952
January	.....	1	.....	6	0	17
February	.....	.....	.....	6	0	0
March	.....	1	8	11	0	9
April	.....	3	10	16	0	19
May	1	6	12	12	8	50
June	2	10	13	10	15	40
July	1	5	11	14	9	36
August	.....	4	.....	20	0	20
September	1	6	10	9	10	67
October	5	4	10	5	50	80
November	.....	3	7	5	0	60
December	.....	1	7	3	0	33

Even though the number of fleas carried is usually small, these parasites must cause great annoyance to the woodrats, which are continually exposed to their attacks. When concentrations in the nest are heavy, damage to young animals might be considerable. I found no evidence that fleas were directly responsible for the death of an adult.

Of the woodrats live-trapped each month (1951-1954 inclusive), the percentages infested with fleas were as follows: January, 18 per cent (of 11); February, 11 per cent (of 9); March, 6 per cent (of 18); April, 13 per cent (of 23); May, 44 per cent (of 25); June, 44 per cent (of 61); July, 27 per cent (of 22); August, 31 per cent (of 26); September, 54 per cent (of 24); October, 64 per cent (of 14); November, 31 per cent (of 16); December, 9 per cent (of 11).

Chiggers

Chiggers are more numerous on woodrats than are any other ectoparasite. In the course of the study, the chiggers collected from woodrats of the study area were of the following ten kinds: *Trombicula lipovskyi* Brennan and Wharton; *Trombicula sylvilagi* Brennan and Wharton; *Trombicula alfreddugèsi* (Oudemans); *Trombicula lipovskyana* Wolfenbarger; *Trombicula trisetica* Loomis

and Crossley; *Euschöngastia peromysci* Ewing; *Euschöngastia diversa* n. sp. Farrell (in press); *Euschöngastia setosa* (Ewing); *Pseudoschöngastia farneri* Lipovsky; *Pseudoschöngastia hungerfordi* Lipovsky. Also, *Trombicula cynos* Ewing from a woodrat taken on another part of the Reservation, and an unnamed species of a genus shortly to be named by Lipovsky, Crossley, and Loomis (in press) from nest material were reported to me by Dr. Richard B. Loomis.

Chiggers were collected in two ways. Most were scraped from the animals where they were grouped in clusters. A second more efficient but more time-consuming method was to place a wire bottomed cage over a large pan of water containing liquid detergent. The woodrat was kept in the cage for two to three days and the chiggers dropped into the water. The detergent prevented them from floating and they could be collected by decanting the water.

Chiggers were observed on the woodrats only when they were present in clusters or in large numbers scattered over the body. The most common site of attachment in winter was in the ear. In most cases clusters were present in both ears but sometimes they were in only one. Other sites of attachment, in order of decreasing preference, were: underside at base of tail; around vaginal orifice; at the bases of teats; inner surfaces of hind legs; on hips and rump; around anus; on scrotum; between the shoulders; and on lower jaw.

Chigger clusters were observed mostly in late summer, fall, and winter, beginning to appear by August and declining in March. In summer they were rarely observed in clusters. Summer chiggers are present but scattered over the body making them difficult to find and almost impossible to collect while handling the animal in the field. In July, 1952, a male was caught that had a few attached around the anus; however, they were not in a large cluster as seen in winter. In June, 1954, two males were observed with chiggers; one with a few on the scrotum and ear, and the other with one on the ear. *T. alfreddugèsi* and *T. lipovskyana* are the two common chiggers in summer infestation although *P. hungerfordi* and *P. farneri* are occasionally found. The remaining chiggers cause infestations only in fall and winter. Why winter chiggers are found in clusters I do not know. Perhaps inactivity is associated with decreased temperatures.

In five nests examined in February, November, and December, chiggers were less abundant than were fleas. As many as three

kinds belonging to two genera have been found in the same cluster. A scraping from the ear of a male on February 8, 1953, had 20 *T. lipovskyi,* six *T. diversa,* three *E. peromysci* in the same cluster. A cluster removed on August 20, 1952, from another male contained 17 *P. hungerfordi,* eight *T. alfreddugèsi,* and two *T. lipovskyana.* In November, 1952, an adult male was placed for three days over water. Four kinds of chiggers were parasitizing this animal. The most numerous was *T. lipovskyi* with approximately 100 being collected. The others, *E. diversa, T. sylvilagi,* and *T. trisectica* were present in smaller numbers.

A subadult male first was observed with a cluster of chiggers in each ear on September 6, 1952. This male was caught several times in July and August, but chiggers were not observed. Chiggers were still present on September 8, October 12, and 25. On November 15, they were scraped from both ears and *T. lipovskyi, T. sylvilagi,* and *E. diversa* were found. Ear scrapings from another male and a female on this same day from the same area both contained *T. lipovskyi* and *T. sylvilagi.* In all three cases *T. lipovskyi* was more numerous than the others. Chiggers had not reinfested the subadult male by November 16 and 22, and in December. The animal was next caught on February 8, 1953, and chiggers were again found in the ears. They were scraped from the right ear and *T. lipovskyi, E. diversa,* and *E. peromysci* found to be present in the same cluster. The rat was captured again on March 14, 1953, but chiggers had not reinfested the ear that had been scraped.

Of the woodrats live-trapped each month (1951-1954 inclusive), the percentages with chiggers were as follows: January, 64 per cent (of 11); February, 33 per cent (of 9); March, 11 per cent (of 18); April, none (of 23); May, none (of 25); June, 3 per cent (of 61); July, 5 per cent (of 22); August, 31 per cent (of 26); September, 67 per cent (of 24); October, 71 per cent (of 14); November, 69 per cent (of 16); December, 64 per cent (of 11).

Ticks

Nymphs and larva of the American dog tick, *Dermacentor variabilis* (Say), were found parasitizing woodrats from the study area. The woodrats were never heavily infested with ticks; the largest number observed on any one animal, 11 total, were on a subadult female, on June 3, 1953. The above mentioned female was caught for the first time on May 28, 1953, at a house constructed at the outcrop, and at that time she had no ticks. She was next caught on May 30, 1953, at the same location, but this time she had

two nymphs, one on either side of the nose among the vibrissae. These were removed. On June 2, 1953, she was captured again at the same location but had no ticks. However, on the following day, June 3, she was found in a trap approximately 175 feet along the outcrop at another house and in the night had acquired 11 ticks, 10 nymphs and one larvae. Three were on the pinnae; one on the right and two on the left. The remainder were on the muzzle. This female seemed to be wandering extensively judging from the intervals between captures and probably she acquired the ticks at sites other than her home.

The usual location for attachment was on the pinnae or the muzzle or both. Nymphs were more abundant than larvae. Of the many ticks collected only one was a larva. Ticks were observed more frequently in June, 1953, than any other time in the study. They were found on woodrats only in the months of May, June, July, August, and September. Only 15 different rats were found harboring these parasites in the entire course of study. More males (10) carried ticks than females. Most (11) of the woodrats infested with ticks were living along the outcrop. An exceptionally mild winter following the exceedingly dry year of 1952 may account for the number of ticks observed in June, 1953. The last half of May, 1953, was unseasonably warm, and June was the second hottest on record up to that time. Lack of ticks in 1951 may be correlated with the fact that precipitation was the heaviest since records were begun in Lawrence in 1869.

Table 7. Woodrats Recorded With Ticks.

Date	Sex and age	Site of attachment	Location of house
May 10, 1952	juvenal female	muzzle	woodland
May 11, 1952	adult male	muzzle	woodland
May 18, 1952	juvenal male	muzzle	woodland
June 28, 1952	adult female	unattached	outcrop
July 31, 1952	subadult male	on shoulder	outcrop
August 20, 1952	adult male	muzzle	outcrop
May 28, 1952	adult male	muzzle	outcrop
June 3, 1953	juvenal female	ear and muzzle	outcrop
June 3, 1953	subadult female	ear and muzzle	outcrop
June 5, 1953	adult male	muzzle	woodland
June 5, 1953	adult male	muzzle	outcrop
June 7, 1953	subadult female	muzzle	outcrop
September 10, 1953	adult male	muzzle	outcrop
June 21, 1954	adult male	ear	outcrop
June 21, 1954	adult male	muzzle	outcrop

Predators

The removal of only a few woodrats from a colony when it is at low ebb would compound the struggle toward increasing numbers of woodrats again. Woodrats that dwell at outcrops are possibly more protected from enemies than are those that live in more open situations. The woodrat is able to carry on all of its activities without having to stray from the outcrop more than a few feet. At almost any time that an enemy is encountered, the woodrat has ready access to many deep crevices and fissures and only a few enemies can pursue the woodrat into such retreats.

On the Reservation and nearby areas, the pilot black snake (*Elaphe obsoleta*), timber rattlesnake (*Crotalus horridus*), horned owl (*Bubo virginianus*), long-tailed weasel (*Mustela frenata*), and spotted skunk (*Spilogale putorius*) are considered to be by far the most important natural enemies. Relationships of each of these predators to the woodrat are discussed in a separate paper (Fitch and Rainey, 1956). Various other predators take woodrats occasionally, and their combined effect is probably important, especially when the population of woodrats is low.

Blue-racers (*Coluber constrictor*) observed in this area were not large enough to overcome an adult woodrat. Newborn woodrats might fall prey to blue-racers. On one occasion, a young blue-racer approximately 10 inches in length was observed sunning itself on a woodrat house. When disturbed it sought shelter by crawling in among the sticks of the house. These snakes have been seen frequently utilizing the shelter of brush piles similar to those in which woodrats commonly construct houses. In most localities, however, the habitats of the blue-racer and the woodrat overlap but little.

Large bull snakes (*Pituophis catenifer*) may prey on woodrats, at least occasionally, where the rats live in hedge rows or open woodland. Bull snakes of all sizes have been seen both along the outcrop and in woodland although the species is more characteristic of grassland. Snakes that prey on woodrats would be able to pursue the animal into most burrows or crevices and kill it by constricting or pressing it against the sides of the burrow. The species was listed by Vorhies and Taylor as an important enemy of the white-throated woodrat in Arizona (1940:508).

Copperheads (*Agkistrodon contortrix*) are fairly common along the outcrop. However, woodrats were not represented among several dozen recorded food items from the Reservation, and must be eaten only rarely if at all. Adult rats are too large to be swallowed by any but unusually large copperheads. On September 30, 1951,

a large copperhead was coiled on top of a woodrat house at a rock fence, and a live-trap only two feet away contained a rat. However, neither the snake nor the rat evidenced interest in the other.

Dr. Rollin H. Baker told of seeing on May 1, 1948, a Cooper's hawk (*Accipiter cooperii*) at the Reservation part of the eastern section of outcrop, flying off with a woodrat. The hawk dropped the rat, which was found to have been killed by having the back of the skull crushed.

The red-tailed hawk (*Buteo jamaicensis*) is one of the most abundant hawks on the study area and throughout eastern Kansas. It has been observed hunting over open and woodland situations of the study area as well as perched in trees. Fitch (1947:150) found that woodrats (*N. fuscipes*) comprised only about 1.1 per cent of the total weight of the food of this hawk in Madera County, California. The daylight hunting of these and other hawks probably makes them unimportant enemies of the woodrat. The less abundant broad-winged hawk, *Buteo platypterus* (Vieillot), may be more important locally because it is inclined to hunt more in woodland.

Marsh hawks (*Circus cyaneus*) are seen occasionally hunting by flying over open situations on the study area. If a woodrat was discovered in the open in the day, it probably could be captured by a marsh hawk, but such occurrences would be exceptional.

Opossums (*Didelphis marsupialis*) are common on the study area and often disturbed traps in attempts to reach either the bait or the captured rat. Hairs found around or on live-traps torn open in a few cases were identified as those of an opossum. Blood indicated that the rat was captured or at least injured. Sandidge (1953:98) recorded no remains of woodrats in 62 stomachs examined from Douglas County. Fitch and Sandidge (1953:322-323) examined 79 scats from the Reservation but found no woodrat remains. The commensal nature of the relation of opossums to woodrats is perhaps more obvious than that of a predator-prey relation. Opossums are frequently found utilizing occupied woodrat houses as daytime retreats. On December 1, 1951, a young opossum was found in the upper part of an occupied woodrat house. It made no attempt to escape as the house was dismantled. A young opossum was found on June 22, 1952, in a live-trap set at a woodrat house. After it was released, it moved directly into the stick house.

Opossums denning along outcrops inhabited by woodrats compete for space and, in some instances, for food. Sandidge (*op. cit.*:

101) found wild grape in three of the stomachs he examined. Fitch and Sandidge (*loc. cit.*) found wild grape to be the most abundant single item in the scats they examined from the Reservation. Hackberries were second in importance. Both are important food items for the woodrat.

Since this study was begun, raccoons (*Procyon lotor*) have been abundant throughout eastern Kansas. Evidence indicates that this animal might be an important predator in local situations where woodrats were available. On the study area, the raccoon constituted a serious pest in its habit of persistently breaking into live-traps. In the course of the study, marauding raccoons repeatedly made live-trapping so unprofitable that operations were suspended for varying lengths of time. Efforts to protect the traps were to no avail. The frequent occurrence of blood on the trap indicated that the rat had been killed and eaten. Hair, tracks, and scats around the trap revealed the raccoon's identity in several instances. Howard J. Stains studied raccoons for the past several years. He examined 738 scats mostly from west-central Douglas County. Two scats in 14 examined from caves in Barber and Comanche counties in south-central Kansas had remains of woodrats (*N. micropus*), but the scats from Douglas County contained none and he informs me that woodrats are not found in the area, in Douglas County, from which the scats were collected.

Fitch and Packard (1955:212) found remains of only two woodrats in an examination of 118 scats of coyotes (*Canis latrans*) collected on the Reservation over a five-year period. Tiemeier (1955: 202) found woodrats (probably including both *N. floridana* and *N. micropus*) in 11 of 871 coyote stomachs collected throughout Kansas over a six-year period.

Investigators in other locales have found that woodrats of various species are taken frequently by coyotes. Sperry (1941:15) recorded woodrats 355 times (4 per cent) in an examination of 8,339 stomachs from 17 states. He states: "Locally, however, they were an important source of food. For example, the coyotes from Texas derived almost a fourth (24 per cent) of their food from cricetids, four-fifths of which were wood rats. In fact, 40 per cent of the Texas coyotes that ate *Neotoma* took nothing else at their last meal." Linsdale and Tevis (1951:196) state that woodrats rank first among all kinds of food taken by coyotes. They recorded woodrat remains 283 times in examining 980 scats. Vorhies and Taylor (1940:508) state: "Notes and other available records of feces examination place the coyote definitely among the more important

enemies of *Neotoma*, while stomach examinations fail to so record it at all." Fitch (1948:74) examined 1,173 scats from the San Joaquin Experimental Range in California and found woodrat (*N. fuscipes*) remains 162 (4.9 per cent) times.

The red fox (*Vulpes fulva*) is not common and the gray fox (*Urocyon cinereoargenteus*) is considered rare in Kansas. Tracks of fox have been seen on the study area. A fox would take a woodrat whenever possible, but this predator is too scarce to be important except perhaps under local conditions.

Escape Reactions

Woodrats, except for young, when forced to leave the house always have predetermined routes of escape. Thorough familiarity with these routes is a definite survival factor. In many cases the reaction is so stereotyped that it can be predicted beforehand. This is more pronounced among rats living in houses constructed at bases of trees. The most common reaction is for the rat to leave the house hurriedly and seek refuge in the tree. Movement is so fast that usually only a flash of brown is seen. The animal invariably stops to survey the situation when it is well up in the tree. If pursuit is continued the rat will move to the uppermost branches or to adjacent trees. If only one tree is available, the rat moves back and forth attempting to remain as far as possible from the pursuer. Footing is always sure, but they have never been observed to make leaps of any great distance from one limb to another. Sometimes the rat seeks refuge in burrows beneath the house. When the house has been partly destroyed, the rat may attempt to leave, and appearing momentarily confused with its surrounding it can be easily captured by hand. Its bewilderment seemingly is due to destruction of its escape routes from the house. Several woodrats attempted to escape from me by traveling on the ground in dense vegetation. However, they immediately took to trees if capture was imminent.

The inability of woodrats to react without hesitation in time of danger when the rats are in unfamiliar surroundings has been observed many times. If released from a live-trap several feet from its house, a rat usually is confused, and frequently seeks any available shelter and remains for several minutes before attempting to return home. Animals traveling across strange territory are circumspect and usually move cautiously with frequent stops. The behavior after release of a subadult male live-trapped on June 24, 1954, is indicative of uncertainty when in strange territory. This

male was new to the section of outcrop where he was trapped and probably was a wanderer from outside the trapping area. Instead of running directly to the outcrop after release as resident rats normally do, he ran away from the ledge and took refuge under a large rock. After remaining there for a few seconds, he moved into the open and stayed there for 10 minutes; his only movements were quivering of the vibrissae and slowly turning the head from side to side as though intently studying the surroundings. He then moved toward a rock fence approximately 40 feet away. He did not run but progressed in a slow methodical fashion, pausing periodically to examine the surroundings. He gave the appearance of being thoroughly lost. If a predator had encountered this woodrat, capture would have been almost certain. A rat released in familiar territory always moved rapidly and without hesitation.

Not only are escape reactions a necessity for the individual, but lives of suckling young depend on these predetermined means of escape. The ability of suckling woodrats to cling to the teats of the mother has been described for other species and is no less developed in *N. floridana*. On July 25, 1954, a house constructed in a hedge row was investigated for occupancy. As soon as the house was disturbed a female with three young attached to her teats dashed out and into the tree. Her movement was quick and sure even with the added weight of the young. She would run along limbs from one part of the tree to another attempting to avoid capture. The young were dragged on their backs over the sharp spines with no apparent injury, and when one of the young lost its grip the mother immediately grasped it in her mouth and carried it in this fashion.

Even where trails are not visible, rats behave in a manner that indicates familiarity with their surroundings; those repeatedly live-trapped at the same site tended to react similarly after each release. The speed of their movements indicates that the escape routine involves conditioned reflexes; it could not be accomplished so efficiently without previous learning. Movement to shelter is direct and not erratic. The fact that young animals are more reluctant to leave a house and are hesitant in their movements after having left provides further evidence that escape reactions are learned.

Wounds varying in nature and severity are frequently observed. Some of these may be from fighting and others may result from encounters with predators. All of the skin had been torn from the top of the left hind foot of a female examined on April 26, 1952.

The bones of the toes and tendons were exposed, but there was no sign of infection. A female on October 14, 1951, had a deep wound 25 millimeters long and 20 millimeters wide on the right thigh. The wound had an odor of putrefaction. Nearly one month later it was much smaller (five by three millimeters) and healing rapidly. On February 17, 1952, a male was also observed to have a large wound (18 by 15 millimeters) on the right thigh. Still another male on October 12, 1952, had a deep cut one inch in length on the left thigh.

In a female observed on May 12, 1952, an osage orange thorn 15 millimeters long had pierced the left ear to approximately half its length, broken off, and the wound had healed holding the thorn firmly in place. The thorn had entered from the anterior side of the ear. When it was removed, scar tissue adhered to the thorn leaving a round orifice in the pinna. When the rat was recaptured on June 13, 1952, the hole had closed.

Infected lesions have been noted several times on woodrats. A male caught on May 15, 1952, had such a lesion on the lower jaw. Surrounding hair was matted by yellowish exudate from the lesion.

One male was completely blind in the right eye but the cause was not evident. The rat seemed to be well adjusted to partial loss of sight because he stayed in the area 210 days after the initial capture.

Another common type of injury was the partial or complete loss of an extremity. Both males and females were live-trapped with varying lengths of their tails missing. The skin of the tail is easily torn away. The exposed part shrivels and drops off in a few days. The ease with which the skin is lost probably saves many woodrats from predators. Bob-tailed woodrats are not much handicapped by the loss. Individuals have been observed maneuvering with seemingly as much agility as woodrats with normal tails. One female was recorded as having lost a toe on the left hind foot.

Commensals and Competitors

The phase of the study directed toward analysis of house structure and related aspects was done mostly in 1952 and 1953. These years were record breaking drought years and woodrat houses were strongly affected. Houses dismantled in these years reflected the results of many consecutive days without rainfall; fine dust had thoroughly permeated the structure including food stores. Possibly for these reasons, the arthropod fauna inside woodrat houses was smaller than would be expected. A few isopods, moths, caterpillars, and other larval forms have been seen in houses parti-

ally dismantled when I was collecting woodrats, but these arthropods were not preserved. Spiders were the invertebrates most commonly found in or on woodrat houses. Other kinds include one hemipteran (*Anasa tristis*), one neuropteran (*Chrysopa* sp.), two coleopterans (*Ptinus* sp. and *Cryptophagus* sp.), and one mollusk (*Stenotrema leai aliciae*). This list of house commensals is far from complete because this phase of study was not investigated in great detail.

Spiders were in nearly all houses dismantled. For some kinds, the stick houses were favorite sites for construction of webs over the surface; others, instead of spinning webs, lived deep within the house. Most abandoned houses soon covered with webs. In fact, the presence of spider webs on entrances is an almost infallible sign that the house is not inhabited by a woodrat. Houses that are occupied never have webs at entrances and frequent addition of sticks, in the course of adding to or repairing the house, usually limit webs to the margins of the base. The following spiders were found in or on woodrat houses: *Herpyllus vasifer, Phidippus audax, Xysticus elegans, Agelenopsis naevia, Micrathena gracilis, Eustala anastera, Lycosa helluo,* and *L. gulosa.* Harvestmen, *Leiobunum vittatum,* are common arachnids in this area and are occasionally seen on woodrat houses.

I found no amphibians in woodrat houses, but Linsdale and Tevis (1951:192) reported three kinds of salamanders and one tree toad from houses in California and Vestal (1938:12) recorded two salamanders and a newt in houses there. The ant-eating frog, *Gastrophryne olivacea,* is sometimes found under rocks on hillsides below rock outcrops inhabited by woodrats.

The box turtle, *Terrapene ornata,* is common on the study area except for that part of it within the Reservation. It was numerous in woodland along the outcrop. A box turtle was in a live-trap at a woodrat house in a brush pile on May 13, 1952; another was in a live-trap on June 21, 1952. After the landowner had burned several of the brush piles containing woodrat houses in the spring of 1954, the shell of a box turtle was found among the ashes of one of the houses.

The five-lined skink, *Eumeces fasciatus,* is the most common reptile on the study area. On June 27, 1952, an adult was seen on a woodrat house into which it escaped. On May 26, 1953, a large male in breeding condition was observed running into a woodrat house. The houses provide the type of shelter required

by the skink, which also feeds on the arthropod fauna found around or in the house.

Great Plains skinks, *Eumeces obsoletus,* are common along the ledges and rocky hillsides. On June 25, 1952, a large adult was caught in a live-trap set at a woodrat house. After it was released it disappeared into the house. These skinks are frequently caught in reptile traps placed along the outcrop.

Ring-necked snakes, *Diadophis punctatus,* are common along the ledges and rocky hillsides below. On May 19, 1951, one was seen lying on a rock near a woodrat house at the outcrop. In July, 1948, a class dismantling woodrat houses under the supervision of Profs. Henry S. Fitch and George H. Lowery, Jr., found a ring-necked snake in the damp soil under a woodrat house.

Birds caught in live-traps set for woodrats include: house wren, *Troglodytes aedon;* catbird, *Dumetella carolinensis;* brown thrasher, *Toxostoma rufum;* song sparrow, *Melospiza melodia;* cardinal, *Richmondena cardinalis;* and Harris' sparrow, *Zonotrichia querula.* Even though birds such as tufted titmice, *Parus bicolor;* black-capped chickadees, *P. atricapillus;* and juncos, *Junco hyemalis,* are frequently seen foraging at woodrat houses, other birds are probably attracted by bait at traps. Mourning doves, *Zenaidura macroura;* yellow-billed cuckoos, *Coccyzus americanus;* crows, *Corvus brachyrhynchos;* blue jays, *Cyanocitta cristata;* cardinals; field sparrows, *Spizella pusilla;* and rose-breasted grosbeaks (*Pheucticus ludovicianus*) have been observed nesting on the study area.

Fox squirrels (*Sciurus niger*) are common over all the study area and compete with the woodrat for food, notably seeds of osage orange. Fox squirrels have been seen many times foraging on the ground near woodrat houses. Bailey (1905:108) found a gray squirrel in a woodrat house (*N. f. rubida*) in Texas.

The white-footed mouse, *Peromyscus leucopus,* is the mammal most commonly associated with woodrats in eastern Kansas. This mouse is more abundant along the rock outcrops than around houses in woodland, and is a common commensal and competitor for space. As a competitor for food the mouse is discussed under the section on food habits. A house dismantled in May, 1954, which was occupied by a female and one young male rat, also harbored a white-footed mouse. On another occasion, a *P. leucopus* dashed from the entrance hole of a woodrat house, paused a few seconds, and dashed back into the house when I made a slight movement. As many as three mice have been live-trapped repeatedly from a single

woodrat house indicating that they lived there; they would dart into the house after release. On July 6, 1951, an adult female woodrat and an adult female *P. leucopus* were together in a live-trap. The woodrat was in the nest box and the mouse at the opposite end of the trap huddled in one corner. After watching for several minutes, it seemed to me that the woodrat was not antagonistic toward the mouse when a distance of approximately one foot separated them. When the mouse was forced close to the nest-box, however, the woodrat slashed out with the forefeet. The mouse easily avoided the blows and retreated to the far end of the trap again. The woodrat made no attempt to follow up the attack. These observations suggested to me that a white-footed mouse could live as a commensal in a house occupied by a woodrat.

Cottontails, *Sylvilagus floridanus,* employ rock outcrops for shelter. On May 9, 1952, a young cottontail was caught in a live-trap set at a woodrat house built in a brush pile. The following day the same trap had caught another cottontail of approximately the same age. On February 8, 1953, a cottontail was flushed from a woodrat house at the outcrop. On December 1, 1951, a cottontail was flushed from a woodrat house that was being dismantled. At another house, a cottontail was flushed from a large opening in one side for several days in succession, and seemingly, it was using it as a regular daytime retreat. Baker (1942:343) found a cottontail in a house of *N. f. rubida* in Texas. The tangles around woodrat houses or the house itself affords good daytime retreats for the cottontail. Competition for food between these two animals is probably slight.

Short-tailed shrews, *Blarina brevicauda,* woodchucks, *Marmota monax,* and meadow jumping mice, *Zapus hudsonius,* have been observed near woodrat houses.

Reproduction and Development

Season of Breeding

In eastern Kansas the season of breeding is from February through August; exceptionally, individuals may breed in September. There are three periods when the incidence of breeding is especially high: late winter (usually early February), late March and early April, and in May. Females that are not fully mature at the onset of the breeding season in late winter may not be bred for the first time until March or April, and females that are not found by a male while they are in heat pass through another complete oestrus cycle before becoming pregnant, thus lagging behind the majority. Chapman (1951:282) reported that *osagensis* in eastern Kansas has spontane-

ous oestrous cycles of three to eight days which continue throughout the year. Hamilton (1953:181) stated: "The *floridana* group, at least in the southeastern states, apparently breeds throughout the year. . . ."

Indications of Breeding in Males

In some males the testes begin to enlarge in late January, but in others this development is later. Both testes may not increase in size at the same time; frequently one lags behind. The testes of most mature males are fully scrotal in position by February and tend to remain in the scrotal sac while the rat is being handled. Sexual activity does not commence until February. When reduction in size begins, the testes usually pass out of the scrotal sac when handled. They may be manipulated back into the sac by palpating the abdominal cavity. Linsdale and Tevis (1951:354) found that viable sperm in the cauda epididymis of *N. fuscipes* formed a conspicuous bulge and that the testes were scrotal. At the peak of reproductive activity in *osagensis,* this bulge is as much as four millimeters thick. The testes are then fully scrotal and do not slip out of the sac. The testes of males undergo slight changes in size throughout the season of breeding and at times are carried in the abdominal cavity. Males with testes that have regressed in size and withdrawn into the abdominal cavity within the season of breeding probably still are capable of fertile matings. In an old male whose testes slipped easily in and out of the scrotal sac the cauda epididymis of both sides was packed with motile sperm. Both testes were being carried in the abdominal cavity. They were 17 millimeters in length and the bulge formed by the cauda epididymis of both testes when forced into the scrotum was slight. The lull in sexual activity in males corresponds with the periods when many females are pregnant.

By late February the testes of most males are carried in the abdominal cavity. In the latter part of March and in April, testes of males are generally fully scrotal, some attaining a maximum length of 25 millimeters. The testes of some are fully scrotal in early May and are abdominal toward the end of the month. Testes of others are scrotal in late May or early June, but most often they are abdominal in June. Even if the testes are forced into the scrotum, the cauda epididymis does not bulge; absence of a bulge might indicate inability to breed. The testes in some individuals are fully scrotal again in late July and in early August. Relatively few males retain the testes in the scrotal sac into September. Oc-

casionally males breed successfully in September. In the entire season of breeding there are a few at any particular time having their testes in the scrotum. Some young adults do not undergo the frequent cyclic changes in size of testes that older males do.

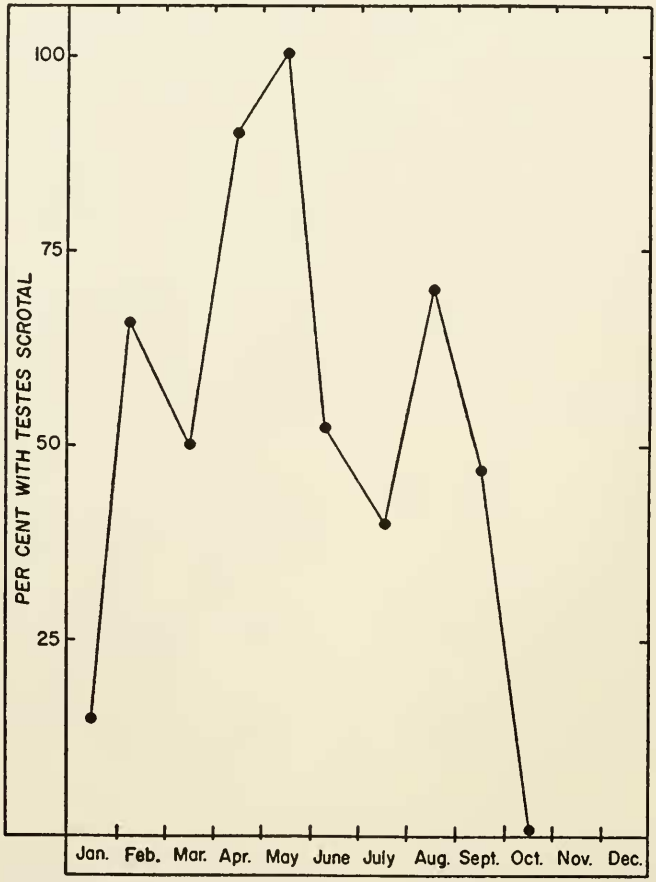


FIG. 3. Record of males with scrotal testes in the period from April, 1951, to June, 1954, represented as per cent of total number of mature males captured.

Reproductive activity among males for the period of study is graphically represented in Figure 3. No significant difference could be detected between successive years.

Sexual maturity develops rapidly in some males, slowly in others. In a young male first captured on July 15, 1952, and then weighing 152 grams, the span of records extended to March 15, 1953, for a

total of 243 days. In this period, the maximum weight attained was 250 grams (March 15, 1953), a gain of only 98 grams. In August, 1952, the testes could be located only by palpating the abdominal cavity and were estimated to be four millimeters long. Even in February and up to the last capture when other males were becoming sexually active, the testes of this male remained small, and they were never observed scrotally. Furthermore, he did no wandering in the breeding season. In the local population of adults there were three males weighing approximately 300 grams which were sexually mature. Sexual maturity was not demonstrable among males in their first season. However, there are indications that rats of second litters or even third litters may mature sexually by February or March the following year.

Indications of Breeding in Females

In periods of sexual inactivity, the vagina is closed, externally the teats are small and hard with flakes of loose epidermis on them, the clitoris is white and not swollen, and hair covers the entire abdomen. The horns of the uterus are soft and are not enlarged. The ovaries are flat, small, and bean-shaped, containing only single and double-layered follicles. In females that are in heat the vaginal orifice is prominent, and the clitoris is enlarged becoming inflamed in the later stages. The vulvar lips are turgid and may stand widely apart or may be in contact with each other. The horns of the uterus are enlarged, firm, and pinkish; the ovaries are enlarged, with pronounced follicular proturbances.

Pregnancy is indicated by an enlarging and softening of the nipples, loss of hair in the mammary area in later stages, especially in the mid-line, and thickening and inflammation of the mammary area. The vaginal orifice may or may not be present. The nipples in later stages are distended and sharply pointed. There is a steady increase in weight, the abdomen is swollen in later stages, and the mammary area is noticeably warmer to the touch than other parts of the body.

A sudden weight loss is indicative of parturition (Fig. 4). The skin of the mammary area of females nursing young is devoid of hair, thickened and wrinkled. When the young are unattached, the teats are not distended. Each teat gives the appearance of being sunk into a crater with a wrinkle around it. The tips may be rough to the touch. The teats are flaccid and can be stretched to 15 millimeters or more in length. Frequently, milk can be forced from the nipples.

In late stages of lactation, hair begins to grow on the mammary area especially in the mid-line, the teats shrink to 3-4 mm. and harden; the skin of the mammary area is no longer thickened nor especially warm to the touch, and the vaginal orifice may be open or closed according to the stage of oestrous. Some females breed while still nursing a litter. A female in late lactation, re-

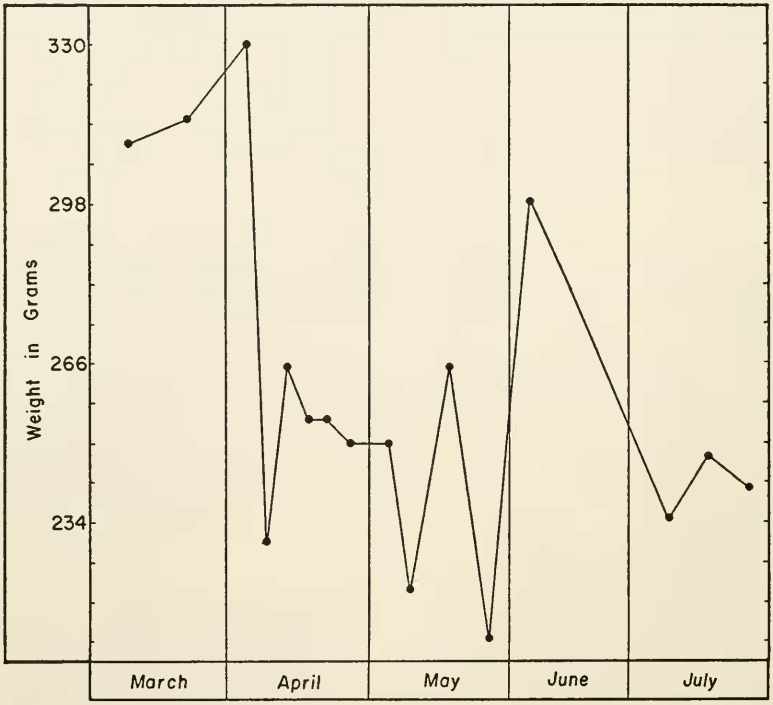


Fig. 4. Weights of an adult female woodrat illustrating pregnancies in early April and June. A litter was born in April and another probably in late June as indicated by losses in weight.

moved from a house in a hedge row on May 16, 1954, had one young, which weighed 61 grams and was approximately one month old. There was a band of new hair growing down the mid-line between the female's teats, the nipples were hard at the tips, and there was a vaginal orifice. There were two swellings in each horn of the uterus which were shown by sectioning to be early embryos. Each of the ovaries had two corpora lutea.

The gestation period is not known for this woodrat. For *N. f. floridana* Pearson (1952:461) reported gestation as probably be-

tween 33 and 39 days, while Hamilton (1953:182) thought it to be approximately six weeks. Wood (1935:108) reported gestation for *N. fuscipes macrotis* as being 33 days. Poole (1940:266) suggested 30 or 36 days for *N. magister,* and Richardson (1943:130) thought gestation to be more than 38 days in *N. albigula.*

On May 11, 1952, a female found in a live-trap with an adult male was in breeding condition; a semi-solid, whitish, translucent plug filled her vagina. She was recaptured 33 days later, on June 13. In this interval she had increased in weight from 152 grams to 216 grams. Her abdomen was swollen and foetuses could be detected by palpation. When caught again eight days later her weight had decreased to 180 grams indicating parturition in the intervening period. If this female was successfully bred by the male while they were in the trap together, gestation was more than 33 days and less than 41 days. A similar vaginal plug was recorded in one other female.

Conclusive evidence that females breed in their first season was not obtained. One young female first caught in late May, 1953, weighed 143 grams and was imperforate. When next captured, on August 15, 1953, she was perforate and her weight had increased to 224 grams; possibly she was pregnant. If females attain sexual maturity near the end of the first season they would have to be of early litters, but it seems that ordinarily breeding is delayed until the next season. The records for all females for which reproductive data are available are presented diagrammatically in Figure 5. In most instances the birth of a litter was assumed when the pregnant female underwent a sharp loss in weight and her mammary area took on the characteristic appearance indicating nursing of young. Some females may have absorbed their embryos, but this could not be readily detected. In each of a few instances, the estimated age of young caught with a female was used to estimate the date of birth of the litter. Again incompleteness of individual records prevent yearly comparisons.

Size and Numbers of Litters

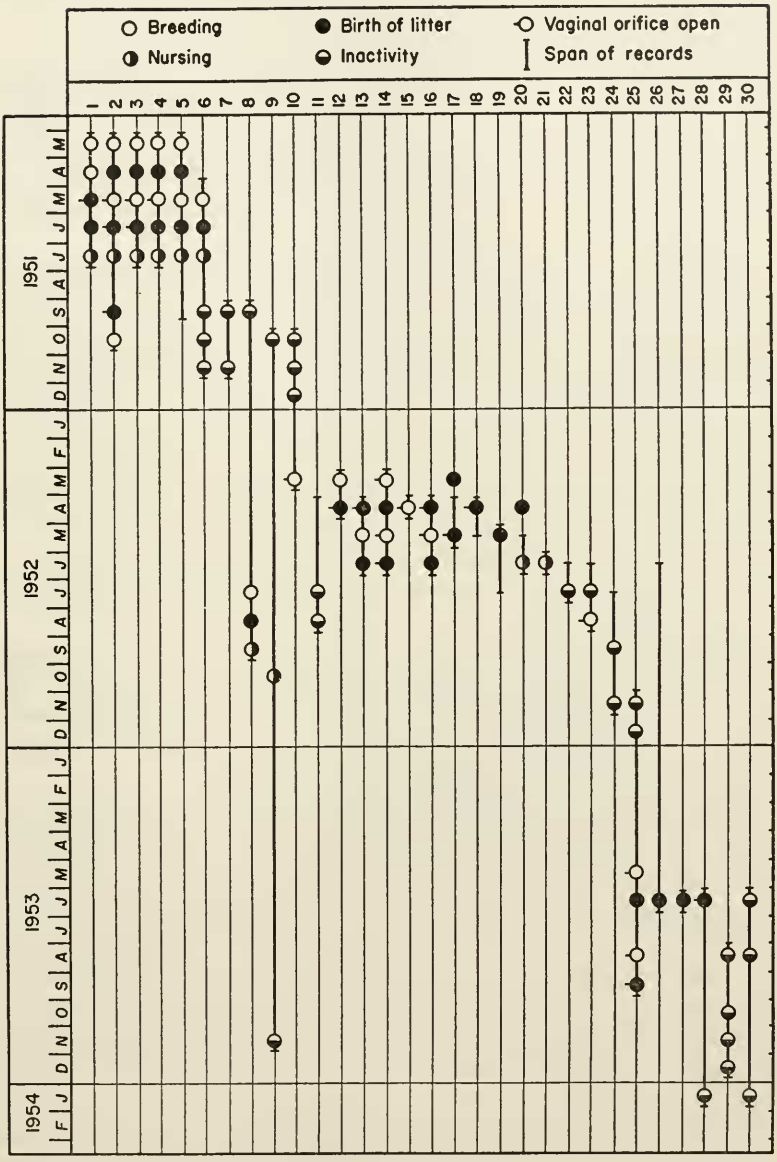
Sizes of litters could rarely be determined with any degree of certainty from live-trapping because the young caught at a house might not represent the entire litter, one or more having been eliminated before weaning. Sometimes it was impossible to determine to which female young belonged, because of the close proximity of several females, especially at the outcrop.

Females have been recorded with from one to five young or

embryos. Seemingly, the most common number of young per litter is two. One female was known to have two litters of two each. Another female was seen nursing two young. A female that died in captivity contained two embryos, one in each uterine horn. When litter size could be ascertained with some certainty by live-trapping, two per litter was the most frequent number. One female was found in a stick house with one young. Another female driven from a house in a hedge row had three young attached to the teats. The label on a study skin in the University of Kansas Museum of Natural History records that there were three embryos. Dr. James Findley, told me of a female examined by him which contained four embryos, two in each uterine horn. A female that I dissected had five embryos, one in the right horn and four in the left. Another female bore a litter of five in captivity. For these 13 litters the average number per litter was 2.7. It is unlikely that all members of litters containing as many as five young survive under natural conditions, because the female has only four teats. The female that reared five in captivity probably was successful because she did not have to leave one of the young. The young lacking a teat would not remain without food for any great length of time. Reports in the literature (Table 8) of sizes of litters and averages for several species of woodrats indicate a general similarity throughout the genus. Most samples average between two and three per litter, but in *N. cinerea* the average is higher than three and in *N. albigula* the average is a little less than two. When there was a sufficiently large sample, the most common number per litter was two—a small number compared to that of many species

Fig. 5. Reproductive data and span of records for all female woodrats, on the study area, for which records are available.

Female 1 seemingly had a litter in early May, 1951, and was bred again almost immediately. Female 2 was gaining weight steadily until the last capture, on October 21, 1951, which might have indicated pregnancy. Female 10 was not bred until some time in March, 1952. Female 11 was in a late stage of lactation on July 16, 1952, and she had young probably in June, 1952. Female 12 may not have survived long enough to bear young. Female 15 was in a live-trap with a breeding male on April 12, 1952, but she was found dead in a trap on May 2, 1952. Female 16 was in a live-trap with a breeding male on May 11, 1952. Two young caught at the house of female 17 were estimated to have been born in late March. A litter was born to female 18 in late April, 1952, but she died from heat exposure on May 2, 1952. Female 19 was in a trap with a young male estimated to have been born in May. A young female, estimated to have been born in April, was in a trap with female 20 on June 24, 1952. Female 20 may have been bred again in August. The teats of female 21 indicated she had nursed a litter in June, 1952. Female 23 may have borne a litter in June, 1952. Female 25 may have had a litter in May, 1953; she seemed to be nursing when caught on May 28, 1953. A litter of five was born in captivity to female 27 on June 9, 1953.


Breeding
Nursing
Birth of litter
Inactivity
Vaginal orifice open
Span of records
1951
1952
1953
1954
J F M A M J J A S O N D
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30

of rodents. Vorhies and Taylor (1940:475) suggested that the low reproductive rate found by them in *N. albigula* resulted from relative freedom from enemies owing to protection by the house, and would apply equally well to other species.

The trapping records of most females were not complete enough to trace individual histories of breeding completely even through one entire season. Neverthless, records of several females show two litters per year, and evidence for the birth of three litters in a season is available for two females, one of which possibly had four litters.

One of these females first caught on March 24, 1951, was pregnant, and she weighed 310 grams on March 28. By April 8, her weight had increased to 315 grams, and she was obviously in a late stage of pregnancy because her abdomen was swollen and foetuses could be detected by palpation. At the next capture six days later, parturition had occurred, with a loss in weight of 100 grams. Possibly this was her second litter of the season, and she became pregnant again sometime in late April or May. By June 3, she weighed 300 grams. The litter was born in early June and she was still nursing by July 1. Seemingly, none of her litter survived because the only young caught near her house was judged to belong to another female.

Another female first caught on March 25, 1951, was pregnant then and bore her litter sometime in April. She was found in a trap with a male in breeding condition on May 11. Seemingly, mating was successful because she had increased in weight to 305 grams by June 3; young were probably born in mid-June.

A female that seemingly had at least three pregnancies in one season was pregnant in March, 1951, when first caught and bore a litter in late April. It is not known whether this was the first or second pregnancy. She became pregnant again in May and bore another litter in June. In later September the appearance of the teats and mammary area indicated that she was then nursing her third litter (or perhaps her fourth if she had borne young in late February or early March). A summary of all young captured in live-traps is included in Table 9. Young that were recorded in other places are included.

The reproductive potential for *N. floridana* is not known precisely, but it is lower than in most other small rodents. Life expectancy for adults is longer than for more prolific species; population turn-over is relatively slow.

TABLE 8. SIZE OF LITTERS AND AVERAGES (OR MODALS) REPORTED IN THE LITERATURE FOR VARIOUS SPECIES OF WOODRATS.

Author	Species	Size	Average	Remarks
Kellogg (1915)	*N. floridana osagensis*	3–6	.....	.....
Dice (1923)	*N. floridana osagensis*	2	.....	Based on one record
Svihla and Svihla (1933)	*N. floridana rubida*	1–4	.....	3–4 most common
Worth (1950)	*N. floridana floridana*	1–4	.....	2–3 most common
Pearson (1952)	*N. floridana floridana*	2–4	.....	3 of 7 litters with 3
Harper (1927)	*N. floridana floridana*	2	.....	one record
Chamberlain (1928)	*N. floridana floridana*	3	.....	one record
Poole (1940)	*N. magister*	.....	2	10 litters
Vorhies and Taylor (1940)	*N. albigula albigula*	.....	1.95	93 litters
Richardson (1943)	*N. albigula*	2–3	.....	3 as maximum
Warren (1926)	*N. albigula albigula*	1–4	.....	.....
Warren (1926)	*N. albigula venusta*	2	.....	one record
Warren (1926)	*N. albigula warreni*	2–3	.....	3 records
Feldman (1935)	*N. albigula albigula*	.....	2 Modal	29 litters
English (1923)	*N. fuscipes*	.....	2.8	.....
Donat (1933)	*N. fuscipes annectens*	2–3	.....	6 litters
Linsdale and Tevis (1951)	*N. fuscipes luciana*	1–4	2 Modal	.....
Vestal (1938)	*N. fuscipes annectens*	1–4	2.6	.....
Gander (1929)	*N. fuscipes macrotis*	3	.....	one record
Warren (1926)	*N. fuscipes streatori*	1–2	.....	.....
Warren (1926)	*N. micropus micropus*	3	.....	one record
Warren (1926)	*N. micropus canescens*	3	.....	one record
Feldman (1935)	*N. micropus canescens*	2	.....	11 litters
Warren (1926)	*N. mexicana fallax*	2–4	.....	.....
Warren (1926)	*N. lepida lepida*	5	.....	one record
Warren (1926)	*N. cinerea cinerea*	1–4	4	.....
Warren (1926)	*N. cinerea saxamans*	3–4	.....	3 litters
Warren (1926)	*N. cinerea arizonae*	4–6	.....	3 litters

Parturition

A female in a late stage of pregnancy was live-trapped on June 6, 1953, brought to the author's home and placed in a cage. She was extremely docile and soon accepted food. By June 8, she was consuming twice as much food as any of the other rats in captivity. Most of the time she was listless and lay stretched out on one side or on her venter with the hind legs extended posteriorly. Seeming restless, she frequently shifted positions. Even when eating she was frequently prone on the floor of the cage supported by her elbows. From 4:00 p. m. June 9, until 12:30 a. m., she spent most of the time in an extremely restless sleep with frequent shifts in position. Occasionally she would eat a small amount but would return directly to the cotton nest and sleep again. At intervals of approximately

Table 9. Summary of Young Born on Study Area and Recorded Elsewhere (*). The Estimated Time of Conception Is Based on a Gestation of Five Weeks.

Sex	Age in days	First capture	Estimated birth date	Estimated time of conception	Number of captures	Span of records	First weight (gms)	Change in weight
Female	30	June 9, 1951	May 19	April 15	3	24	.....	.....
Male	59	July 3, 1951	May 5	April 1	8	152	108	192
Male	38	Oct. 14, 1951	Sept. 6	Aug. 2	2	7	77	12
Male	33	Apr. 26, 1952	Mar. 24	Feb. 18	2	2	67	–3
Female	33	Apr. 27, 1952	Mar. 24	Feb. 18	9	106	63	77
Male	33	May 8, 1952	April 5	Mar. 2	12	392	64	159
Male	48	June 13, 1952	May 6	April 2	1	0	71	0
Male	60	June 18, 1952	April 19	Mar. 9	5	8	103	–4
Female	60	June 18, 1952	April 19	Mar. 9	5	351	90	106
Male	28	June 19, 1952	May 22	April 18	1	0	51	0
Male	45	June 19, 1952	May 5	April 1	3	23	80	15
Female	69	June 19, 1952	April 11	Mar. 7	2	5	114	0
Female	45	June 20, 1952	May 5	April 1	9	83	96	64
Male	84	June 21, 1952	Mar. 29	Feb. 23	1	0	130	0
Female	94	June 22, 1952	Mar. 20	Feb. 14	1	0	140	0
Male	59	June 26, 1952	April 28	Mar. 25	2	2	104	2
Male	99	July 15, 1952	April 7	Mar. 4	24	243	156	98
Male	64	Aug. 11, 1952	June 8	May 5	1	0	112	0
Female	89	Sept. 12, 1952	June 15	May 12	2	149	136	13
Female	?	May 28, 1953	?	?	8	79	143	81
Female	63	June 3, 1953	April 1	Feb. 25	8	13	113	3
Female	69	June 4, 1953	Mar. 27	Feb. 21	1	0	116	0
Female	44	June 5, 1953	April 22	Mar. 19	6	9	83	0
Male	44	June 5, 1953	April 22	Mar. 19	1	0	94	0
Female	69	June 5, 1953	Mar. 28	Feb. 22	10	216	119	72
*Female	50	Nov. 10, 1953	Sept. 21	Aug. 18	.....	.....	98	.....
*Male	29	May 16, 1954	April 17	Mar. 14	.....	.....	61	.....
*Male	19	Mar. 28, 1954	Mar. 9	Feb. 3	.....	.....	42	.....
*Female	19	Mar. 28, 1954	Mar. 9	Feb. 3	.....	.....	44	.....

three to four minutes, movement of the foetuses would cause a bulge to appear in the abdominal region. The instant preceding this movement by the young, the rear legs of the female would suddenly retract. Perhaps this was a sign of pain. The interval between movements of the young became progressively shorter. The vaginal orifice was observed to be open. Observations were terminated at 12:30 A. M., on June 9, and when resumed at 7:00 A. M., four young had been born, and all were attached to nipples. The female was giving birth to a fifth at 7:05 A. M. She was in an upright position with all feet on the floor of the cage. The female remained for 10 minutes in an upright position, bent with the head between the rear legs, and began chewing and licking. She turned permitting a view of the newly born young and appeared to bite off the attached piece of umbilical cord. For two hours following birth, the last young remained uncleaned and unattached.

Newborn young

The newborn woodrats were slate gray on the back, about halfway down the sides and on the head, except for the tip of the muzzle, which was pinkish. Scattered light-colored hairs over the back were visible only under magnification. The underparts were pale owing to a sparse covering of white hairs. The dorsal part of the tail was dark near the base with pigmentation decreasing in intensity toward the distal end. The tail was wrinkled so that it appeared segmented. The pinnae were folded downward over the external auditory meatus. The vibrissae were four to five millimeters long. The eyes were closed. Claws were evident but small. Both upper and lower incisors had erupted. Hamilton (1952:186) has described and pictured incisors of newborn young of *N. f. floridana* and discussed their adaptation for attachment to the nipples. Young are capable of moving slowly by actively wriggling almost as soon as born. Hamilton (*loc. cit.*) states: "Sex is readily determined at birth, the four mammae being evident in the young females." This was not observed by me.

Care of young

Females nursing young frequently leave the house when disturbed, to seek refuge in a tree with the young attached to the teats. Young that are near weaning have not been observed to cling thus to the teats and the mother abandons them. Females in captivity will hover over the young protectively but will not actively defend them, and upon provocation will leave them if they are unattached. When young left in the nest while the mother was in another part

of the cage were caused to squeal the mother would not return to them but would retreat to one corner. As soon as the disturbance ceased, she would return to the young.

The female that bore and reared the litter in captivity spent most of her time in the first month nursing the young. In nursing, she most frequently lay on her side. At times she would lie on her abdomen with the posterior part of the body elevated allowing space for the young to suckle. She frequently cleaned them by licking, turning them with her front feet. On the second day after birth the mother was observed to remove them from the teats by pushing on their shoulders or hips. After the young were older (18 days) she would dislodge them by turning in a small circle pushing with both front feet and her nose. Several rotations were required to loosen all five young. Because the four teats did not accommodate all the young, one, not always the same individual, was attached to the clitoris which soon became greatly enlarged probably from irritation by the suckling young. The mother rotated the young allowing all to feed. The mother was never observed to display irritation toward the young for the period that they were together.

Development and Growth

The five young (three males, two females) averaged 10.4 grams in weight two hours after birth. The largest weighed 11 grams and the smallest 9.8 grams. They averaged 87.4 millimeters in total length. Hamilton (1953:183) recorded average total length for 21 newborn *N. f. floridana* as 93 millimeters and average weight as 14 grams.

The pinnae of all young unfolded and erected the second day, although the external auditory meatus remained closed. Also by the second day, the dorsum was almost black. The underparts were reddish. The young characteristically held their tails elevated in an arc. When they lay sleeping unattached to a nipple, they twitched, causing the entire body to move, at intervals of 20 to 45 seconds. A similar jerking motion was observed when they were attached to teats but was limited to the hind legs.

On the fourth day, the dorsum, head, and outer surface of the legs had a uniform covering of short black hair. There were also longer, light gray hairs scattered on the back. The abdominal region had short white hairs visible only with magnification. The inside of the pinnae had a sparse covering of short, straight gray hairs. The external auditory canal had not opened. The eyes, still

closed, protruded more than at birth. The incisors were unchanged and almost translucent under a dissecting microscope. The posterior pads of the rear feet had acquired a light gray tinge. Even by this time, nipples were not evident. The young made a wheezing sound in breathing when they were not attached to a nipple. As much time as the mother would allow was spent in nursing. While the young were still attached, the mother frequently cleaned them by vigorously licking them. She usually licked the anal region more gently. The young attached so firmly to the nipples that they could be removed only by exerting a firm, steady pull and twisting them. When the young were replaced with the mother, they squealed loudly and actively squirmed to find a nipple.

On the eighth day the young that was attached to the clitoris was extremely difficult to remove, and the clitoris was lacerated by both upper and lower incisors. By this date the fur had thickened considerably. The vibrissae were approximately 10 millimeters long and when they were touched the young folded them along-side the head. The hair on the abdomen was also thicker. The tails were distinctly bicolor with short black hairs on the upper surface and white hairs on the lower surface. The wrinkles were not as evident as they had been at birth. The soles of the hind feet were deeply pigmented while no pigmentation was visible on the front feet. Hairs on the inner surface of the pinnae were more numerous and longer; the external auditory meatus was still closed. The upper incisors were approximately half the length of the lower. The area around the vibrissae was not so pinkish as earlier. The young were capable of active movement but had difficulty in forward progression. The eyes had increased in size and appeared to be closed as if sleeping. The wheeze when breathing was accompanied by an audible squeak.

By the fifteenth day, the eyes of all the young had opened. As far as could be determined while they were attached, the eyes had not completely opened the previous day. The young were able to run with well-coordinated movements, and spent more time unattached foraging about the cage. The incisors were almost together but the lower incisors were still about twice as long as the upper. The hair on the ears had increased in length. The dorsum appeared more gray but was still darker than the sides. This dark hair was prominent on the outer surface of the legs down to the wrist and the ankle. The region around the vibrissae had lost the pink color. The young urinated copiously and the feces were still formless and light brown.

On the sixteenth day, one young was observed attempting to eat a sunflower seed. However, it was unable to break through the seed coat. The young were able to clean and scratch themselves. Later the same day, one was observed eating lettuce. The food was held in the front teeth in the characteristic adult fashion. On the following day, one young woodrat exhibited aggressiveness in biting the finger of the person handling it.

By the twentieth day all the young took solid food even though they still nursed. They were able to climb the sides of the cage. Except for increasing size, no significant change had taken place.

At six weeks of age (average weight, 86.4 grams) they still occasionally attached to the nipples although the size of the nipples indicated lactation had stopped. One was observed attached when

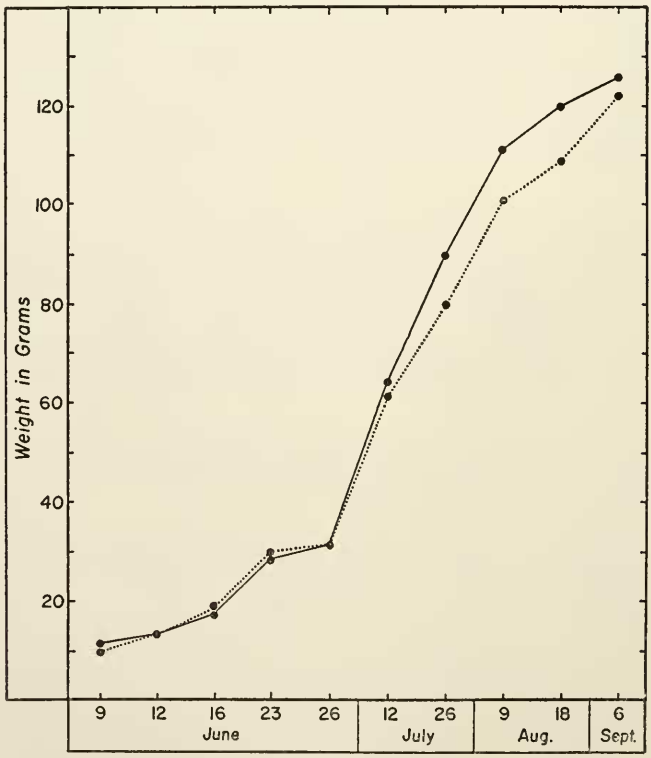


Fig. 6. Weights of a litter of five young (three males and two females) born and raised in captivity. The solid line represents average weights of the males; the broken line indicates average weights for the females.

it was ten weeks old but under natural conditions suckling probably is discontinued earlier.

Woodrats increase rapidly in weight from birth to approximately three months of age (Figure 6), thereafter the rate of increase slackens and full adult weight usually is not attained until the animal reaches an age of eight months or more. However, individuals occasionally undergo extremely rapid growth and reach adult size in a much shorter time. One male woodrat that weighed 108 grams when first caught on July 3, 1951, was estimated to have been born in early May. He was last captured 152 days later on December 2, 1951. By then his weight was 300 grams, an increase of 1.2

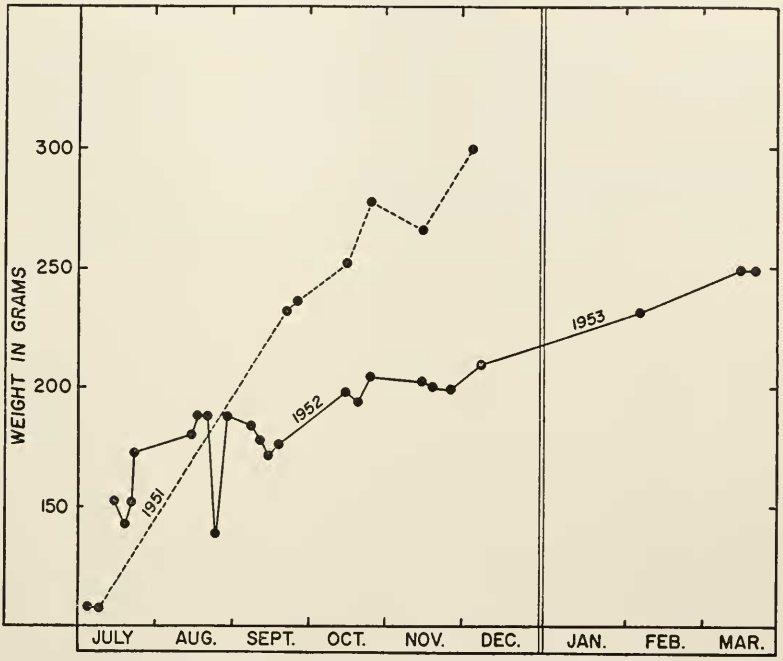


FIG. 7. Differences in growth of two young males. The male represented by the broken line was born in 1951 (probably in May) and lived only until the following December. The second male (solid line) was born in 1952 and was last caught on March 15, 1953.

grams per day on the average, to a size near the maximum. Figure 7 illustrates the comparison between the growth of this male and another young male that required a considerably longer time to reach adult size. The latter male first captured on July 15, 1952, and weighing 152 grams, was estimated to have been born in late

March or early April. He was last caught on March 15, 1953 (243 days), and weighed 250 grams having gained 98 grams, an average daily increase of only .4 grams. Figure 8 illustrates still another instance in which growth was perhaps even more retarded. This male was first caught on May 8, 1952, and weighed 64 grams. When last captured 392 days later the weight had increased 159 grams; this also was an average daily increase of .4 grams. However, the weight of 223 grams at last capture when more than a year old was still less than that of most adult males. Females tend to lag slightly behind males in weight gains. Possibly drought in 1952 and 1953 retarded growth.

Survival of Young

Of 27 young (average weight 103.4 grams) captured on the study area, six were caught only one time. The average span of records for the young caught more than one time was 25.5 days. Of the six that were known to have reached adult size, three seemingly did not survive long enough to breed. So far as known, of the 27 young only 11.1 per cent survived to contribute to maintenance of the local population. A young male first caught on

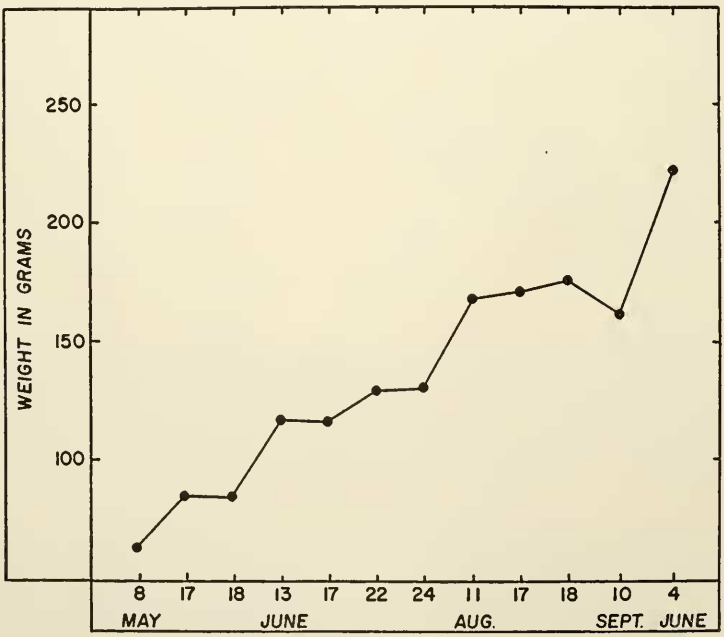


Fig. 8. Growth of a young male born in 1952 (probably in April) that survived to sexual maturity. He was last captured on June 4, 1953.

July 15, 1952, was last seen 243 days later on March 15, 1953; another male survived 392 days and a female survived 331 days and bore at least one litter of young. None of the young live-trapped along the western section of outcrop were known to have survived to sexual maturity.

The minimum number of young that should have been produced from known pregnancies greatly exceeded the number caught in traps. Most of those unaccounted for probably did not survive until weaning. Perhaps resorption of embryos is also an important factor.

The poor survival of young after weaning may be partly explained by their inability to establish new houses owing to scarcity of building sites. This would be more pronounced in the woodland section where the brush heaps were limited. Young are probably more susceptible to natural enemies than adults. Small to medium sized snakes that would be unable to capture and overcome adults could take young rats. Some of the young possibly perished while the mother was in a live-trap over night for periods up to 12 to 14 hours. Extremely young rats might be killed from exposure especially in cold weather in March.

Changes in Pelage

The pelage of woodrats approximately one month old has a faint brown wash that is more noticeable on the cheeks. The first molt begins when young are five to six weeks old. The molt starts on the abdomen, chest, and throat and progresses dorsally. The new brown hair is usually first discernible on the outer sides of the front legs and also on the cheeks. The growth of new hair progresses more rapidly ventrodorsally on the middle of the body. However, new brown hair usually is observed on the hips before the molt reaches the mid-dorsal line. After reaching that line the molt progresses more slowly anteriorly and posteriorly. A narrow band of new hair grows posteriorly on the sides of the head passing behind the ears to meet in the mid-line between the ears. New hair grows back over the forehead to meet that coming in behind the ears. The molt ends in a small zone across the back about midway on the body leaving an anterior region and a posterior region. Just previous to this stage the triangular anterior area connects to the part on the rump by a narrow band down the back. After separation, the anterior region is triangular; the widest part is across the shoulders. The point of the triangle extends down the mid-dorsal line. The posterior region lies across

the rump. In some individuals the rump is the last area to molt whereas in other individuals the last to molt is a small spot between the shoulders. The brown color of new hair after this molt has been completed is not so intense as in adult pelage. Generally, it also lacks the Pinkish-Cinnamon color especially along the lateral line.

The time and rate at which the rat first molts varies with individuals as well as with size and age. One young male of 103 grams first caught on June 18, 1952, had new brown hair visible on the face, sides of front legs, and flanks. In addition, there was new brown hair on the rump and upper parts of the hips which could be seen only by parting the old gray hair. Eight days later, the first molt was considered to be complete. A young female of 90 grams caught the same day was in a later stage of molt but completed it about the same time as the male. New brown hair was visible without parting the old fur on the flanks and arms. However, by parting the old hair new brown hair could be seen over the back and rump. Ten days later she had completed this initial molt. Another young female (63 grams) seemed not to be molting when first caught on April 27, 1952. However, three days later new brown fur could be seen by parting the old fur on the sides and back but not on the rump. Possibly the molt was in progress when she was first captured, but it was overlooked owing to difficulty of detecting new hair on the abdomen. By May 8, 1952, new hair was observed close to the skin on the rump. Brown hair was visible on the face, flanks, and behind the ears. Two days later the over-all appearance of the dorsal pelage was dusky, washed with a brown tinge. By May 16, the only gray left was between the shoulders. At this date her weight was 109 grams. Another male (64 grams) was in about the same stage of molt on May 8, 1952, as the above female when she was first caught. When next caught on June 13, 1952, the first molt was recorded as complete. He then weighed 118 grams.

The pattern of the second molt which immediately follows the initial molt is not so well known owing to inadequate records of individuals. Linsdale and Tevis (1951:455-456) described a second molt from "immature" to "subadult" pelage for the dusky-footed woodrat. The initial molt of *floridana* described herein agrees closely with the initial molt (juvenal to immature) described by Linsdale and Tevis for *N. fuscipes*. However, I was unable to establish a pattern in the second molt that agrees with the similar stage described by them. They described the second molt as starting on the rump and progressing uniformly forward. A male under observation from July 15 to 31, 1952 acquired no new hair, but gained in weight from 152 to 172 grams. New hair was observed on the flanks at the "lateral line" from August 15 (181 grams), until August 21. When next caught on September 6, the new hair was showing through on the flanks and new younger hair was observed over the thighs. By September 12 (177 grams) new hair was visible on the front legs, flanks, anterior one-half of the thighs, and behind the ears, and could be seen on the rump by parting the old pelage. On the basis of this rat's size when first caught this molt was thought to be his second, and the pattern was similar to that of the initial molt. One month later when this male weighed 198 grams, he was molting in patches; probably this was the third molt preceding attainment of adult pelage.

A young female first caught on August 16, 1953, weighed 150 grams and was in molt, judged to be her second, on September 9, 1953. There was new hair close to the skin on the mid-dorsal line, up to the shoulders and for a short distance on either side of the mid-line. New hair was visible at the "lateral line" without parting the old fur and obviously represented older hair than on the back. No new hair was observed on the rump. Progression of the molt seemed to be principally from the ventral to the dorsal surface.

The next change in pelage, which occurs in patches with no regular pattern, results in acquisition of the adult pelage. Seasonal molts of adults also occur in patches. When old adults undergo a molt, the worn pelage sheds readily especially when the animal is handled. In several instances, patches of new hair were still close to the skin but the old hair had already fallen. This rapid shedding of old hair while new hair is short results in a ragged appearance.

Movements

Home range, territoriality, shifts from normal foraging range, dispersal of young, longevity, and some related matters are treated in another paper by Fitch and Rainey (1956:499-533).

Populations

Numbers and Ratios on Study Area

In the period from March 24, 1951, to June 24, 1954, 105 woodrats were live-trapped 660 times on the area of study. The woodrats were not abundant at the beginning and they decreased in numbers throughout the period of study. In February, 1955, one night of sampling did not yield any captures. The population in the woodland section was completely eradicated as a result of burning of most of the houses by the landowner. Two houses at the eastern section of the outcrop with long histories of occupancy were dismantled in February, 1955, and found to be abandoned. Most of the live-trapping was done in 1951 and 1952. Table 10 summarizes total trap nights for the three areas for the four years. Table 11 summarizes trapping records for the years 1951, 1952, and 1953. Table 12 illustrates higher mortality in June than other months involving chiefly the young. Trapping was not continuous. It is believed that live-trapping, especially when carried on for several succeeding nights, results in the capture of most individuals present in the area, but some few exceptionally wary individuals may not enter traps. From the data obtained, numbers present each month and annual trends can be demonstrated with a fairly high degree of accuracy.

Of the 105 woodrats live-trapped, 47 (44.7 percent) were females and 58 (55.3 percent) were males. Females were caught 362 times and males were caught 298 times. This difference results from

males tending to wander more than females. Females tend to be caught repeatedly at one house. The difference in sex ratio is not considered to be significant. Yearly sex ratios including only newly marked rats are: 1951, 17 males and 11 females; 1952, 28 males and 25 females; and 1953, six males and 11 females.

Table 10. Summary of Trap-nights for the Three Areas of the Tract Studied.

Section	1951	1952	1953	1954	Totals
Eastern area	823	592	317	70	1,802
Western area	.....	150	120	42	312
Woodland	.....	566	58	4	628
Totals	823	1,308	495	116	2,742

On the basis of pelage color, weight, general body proportions, and in some instances, time of year when first captured, woodrats were classified in three age groups: juveniles, subadults, and adults. Even though three molts were detected from young to adult, this feature could not be used to distinguish a fourth age group as was done by Linsdale and Tevis (1951:450) for *N. fuscipes*. In this report, subadults are considered to undergo one molt before attaining adult pelage.

Woodrats were recognized as being juveniles until they completed their first molt. The gray juvenal pelage is easy to recognize because it contrasts with any new brown hair which might be present. Generally, weights were less than 150 grams although some individuals weighed more when they completed the first molt. On the other hand, some females weighing approximately 145 grams were diagnosed as subadults.

The brown of subadult pelage is not so intense as in adult pelage. Subadult pelage lacks the Pinkish-Cinnamon color along the "lateral line" which is usually prominent in adults. Adults are more robust and muscular than subadults. The skin of subadults fits loosely and is thinner. Subadult males weigh from 170 to approximately 250 grams and subadult females from approximately 150 to 200 grams. Subadults first caught in autumn or early winter usually were young adults by the following February or March. Rats were classed as adults when they showed first external signs of sexual maturity. Others first caught in nonbreeding season were called adults because of size, weight, and color of pelage. It could be safely as-

TABLE 11. SUMMARY OF TRAPPING RECORDS FOR THE ENTIRE STUDY AREA, FOR 1951, 1952, 1953.

Date	New individuals						Previously marked		Total captures	Total trap nights
	Males			Females			Males	Females		
	J*	SA**	A***	J	SA	A				
1951										
Mar.	.....	.....	3	.....	.....	5	.....	.....	13	71
April	.....	.....	3	.....	.....	1	1	5	31	182
May	.....	.....	2	.....	.....	.....	4	6	66	180
June	.....	.....	.....	1	.....	.....	6	6	33	100
July	1	.....	.....	.....	.....	.....	3	7	30	140
Aug.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Sept.	.....	2	.....	.....	2	.....	3	3	15	40
Oct.	1	2	1	.....	.....	2	2	2	16	44
Nov.	.....	.....	1	.....	.....	.....	5	1	7	22
Dec.	.....	.....	1	.....	.....	.....	6	.....	9	44
Totals	2	4	11	1	2	8	.....	.....	220	823
1952										
Jan.	.....	.....	.....	.....	.....	.....	5	1	10	110
Feb.	.....	1	.....	.....	.....	.....	3	2	14	132
Mar.	.....	.....	4	.....	1	4	.....	2	15	95
April	1	.....	4	1	.....	3	3	4	42	90
May	1	.....	1	.....	.....	1	2	7	41	140
June	6	.....	1	4	.....	6	3	5	59	237
July	1	1	1	1	1	1	2	6	39	135
Aug.	1	2	3	.....	.....	.....	7	7	43	190
Sept.	.....	.....	.....	.....	1	.....	4	4	15	137
Oct.	.....	.....	.....	.....	.....	.....	4	1	13	40
Nov.	.....	1	.....	.....	1	.....	3	1	14	28
Dec.	.....	.....	.....	.....	.....	.....	2	1	4	14
Totals	10	5	14	6	4	15	.....	.....	309	1,308
1953										
Jan.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Feb.	.....	.....	.....	.....	.....	.....	2	1	3	14
Mar.	.....	.....	.....	.....	.....	.....	2	.....	3	44
April	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
May	.....	.....	1	1	.....	.....	1	1	6	35
June	2	.....	.....	4	.....	3	5	3	62	247
July	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Aug.	.....	.....	.....	.....	2	.....	1	3	6	34
Sept.	.....	1	1	.....	1	.....	1	2	13	49
Oct.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Nov.	.....	.....	.....	.....	.....	.....	1	2	9	60
Dec.	.....	.....	.....	.....	.....	.....	1	1	4	12
Totals	2	1	2	5	3	3	.....	.....	106	495

* Juvenile ** Subadult *** Adult

Table 12. Disappearance of Woodrats by Months. Records for June, 1954, Not Included Because Field Operations Were Terminated That Month.

Date	1951	1952	1953	1954	Totals	Per cent
January	.....	3	1	2	6	6.3
February	.....	3	.....	.....	3	3.2
March	2	1	2	.....	5	5.3
April	.....	7	.....	.....	7	7.4
May	.....	3	1	.....	4	4.2
June	2	15	10	.....	27	28.4
July	6	5	.....	.....	11	11.5
August	.....	7	3	.....	10	10.5
September	2	4	3	.....	9	9.5
October	2	1	.....	.....	3	3.2
November	2	3	1	.....	6	6.3
December	3	.....	1	.....	4	4.2

sumed that they were sexually mature. In one young subadult male unusually early enlargement of the testes to 5 millimeters occurred in his first summer when he weighed 171 grams, but the testes did not descend into the scrotum and he was not considered to be fertile. In general, woodrats mature sexually somewhat before they show other morphological traits characteristic of adults.

Population Trends

When live-trapping was begun in March, 1951, and for the remainder of the year, trap sites were only at the eastern section of the outcrop. In the latter part of March, 1952, live-trapping was begun in the woodland. Several traps were moved to the western section in June, 1952. Because of the small numbers involved, population trends were partly obscured by such factors as trap-raiding and deaths in traps from heat prostration. However, it was obvious that the woodrats were not able to recover sufficiently to replace losses. Figure 9 illustrates increasing difficulty in live-trapping woodrats by 1953 owing to low numbers.

The populations at the western section of outcrop and at the houses in the nearby woodland were considered separately for purposes of convenience. However, especially among the males, there was probably more interpopulation flow than the records show. The permanent occupants of the houses in the woodland and at the outcrop were mostly females. In the breeding season it seemed that most males were wandering in search of females. Of the 23 rats caught at the western section of outcrop, only four were adult males and three of these had moved up from the woodland houses.

The disappearance of adult males may have been correlated with movements between the outcrop and the woodland houses. Such trips were hazardous because there were no available routes having abundant overhead cover. Trees were almost the only places of refuge in time of danger.

In the spring of 1951, the colony of woodrats at the eastern section of outcrop was probably not at its peak, but population den-

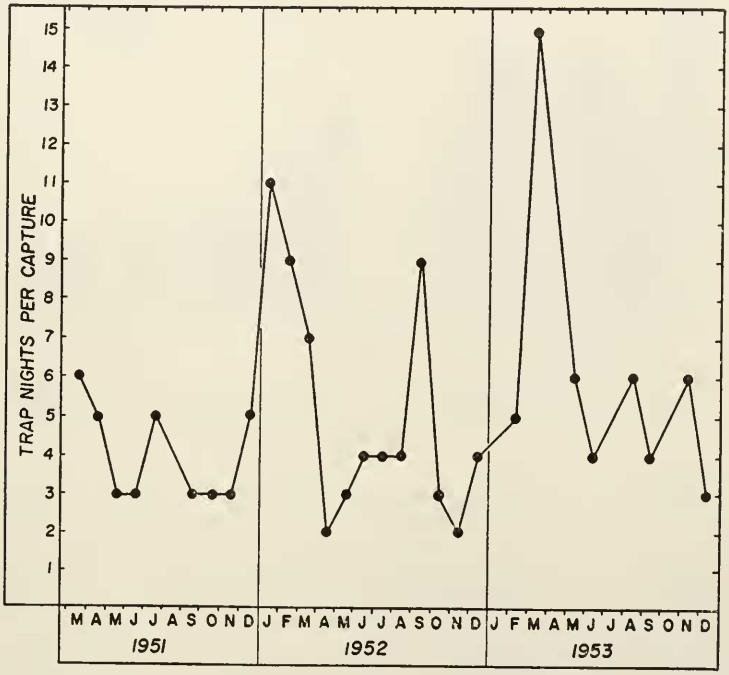


FIG. 9. Number of trap-nights required for each capture for each month that live-trapping was done on the study area.

sity remained greater there than in most other areas (Figure 10). There were from 10 to 12 adults present and all appeared to be in good health. Most of the females were recorded as being pregnant. However, there was a conspicuous absence of first-litter young. As previously mentioned they may have died of exposure while the mothers were in traps. March was cool, the average temperature at Lawrence being 4.3° Fahrenheit less than average. Of the 19 rats that were adults when first caught in 1951, 14 (64.3 per cent) did not survive into 1952. Three of the six subadults that moved into the area did not survive until 1952, and only one of the three

subadults that survived reached sexual maturity. Excess moisture in June and July at the time when many young were beginning to disperse may have eliminated many. Precipitation at Lawrence was 6.98 inches above average for June and 10.37 inches above average for July. Newly weaned young may be more susceptible to extremes of moisture than are adults.

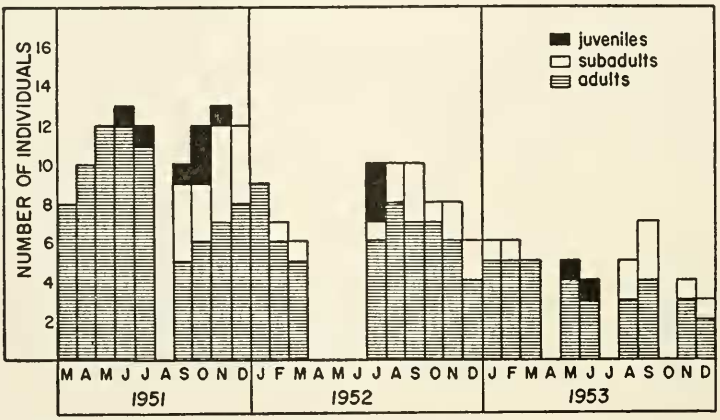


Fig. 10. Trends in the population of woodrats at the eastern section of outcrop in 1951, 1952, and 1953. Diagram based on live-trapping records.

There were only three females and six males present at the beginning of 1952. One of the females was too young to breed in February and disappeared in March and another female left the area, so that only one breeding female remained and five of the six males likewise disappeared before the start of the breeding season. In March, 1952, results from live-trapping at the eastern section of outcrop were so poor (Figure 11) that operations were halted there, and in April, May and June, trapping was done in the woodland instead. In the summer of 1952, the population at the eastern section was increased slightly by immigrants and juveniles. In early autumn of 1952, the population remained stable, but several rats disappeared in late autumn, and by December, there were only three females and three males living at the outcrop. One female disappeared before breeding the next season (February, 1953), two left the area, and were not captured again until May 28, 1953, and November, 1953, respectively. In 1952, the failure of the young to survive was notable, as only one, a young female attained adult size. Of the 22 individuals caught in 1952, 73 per cent did not

survive into 1953. Unusual weather may have caused heavy mortality in young and may even have caused losses among the adults. June, which usually has more precipitation than any other month of the year, was the second driest on record for the state.

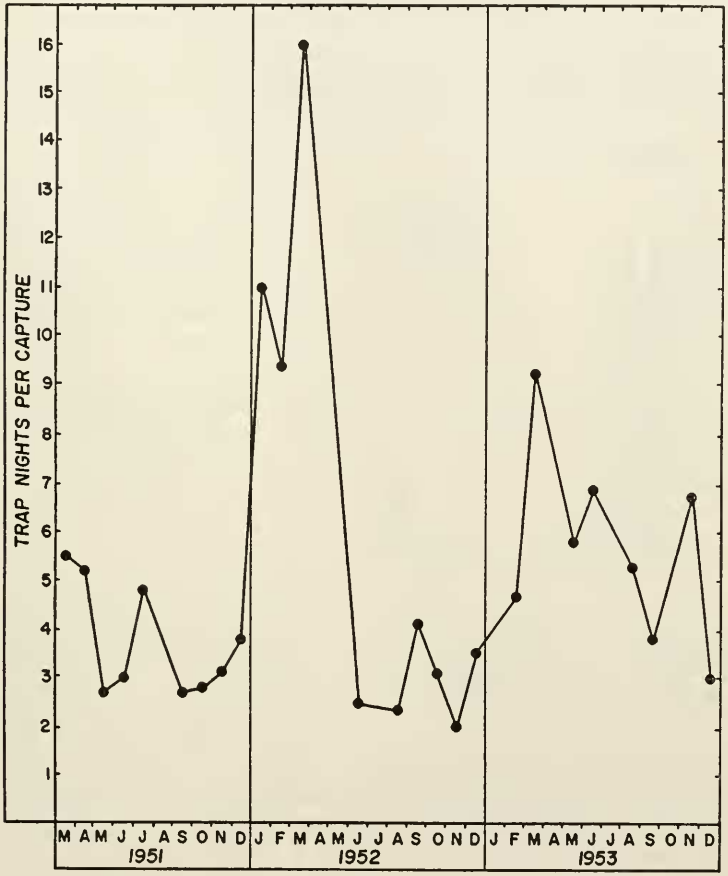


FIG. 11. Number of trap-nights required for each capture for each month that live-trapping was done on the eastern section of outcrop of the study area.

The downward trend continued through 1953, another year of drought. In March, 1953, no females were caught, but two that had been previously marked probably were present as they were recaptured subsequently. The only juvenile recorded was caught in May and it did not survive to adulthood. The population was increased in September by the immigration of one new adult and

two new subadults. However, neither of the latter survived. None of the females caught in 1953 survived into 1954.

The population of woodrats inhabiting the eleven houses in the woodland underwent an even more disastrous decline in 1952 (Figure 12). Eventually this population disappeared completely and most of the houses were destroyed by the landowner. When trapping of this population was begun on March 30, 1952, there was a well-established, stable population of at least 15 breeding adults (eight females and seven males). There must have been keen competition for houses because as soon as a house was vacated by one rat, another would move in. Successful breeding in February or March, was indicated by the capture of two juveniles in April, neither of which survived to sexual maturity. Of the 14 adults caught in April, six (five of them males) were not caught the following month. One of these died in a trap. In May, three adult females were lost; two died in traps and the third presumably was taken by a predator.

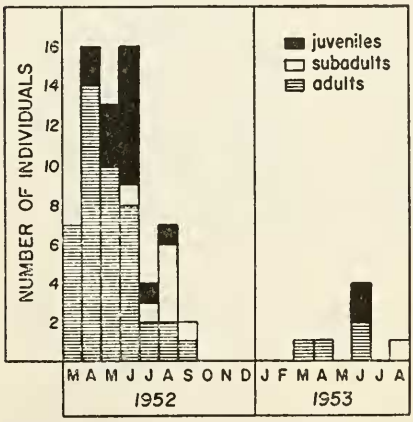


Fig. 12. Trends in the population of woodrats at the woodland section of the study area in 1952 and 1953.. Diagram based on live-trapping records.

The population was greatly decreased in June and loss was especially heavy among juveniles; five of the seven caught disappeared during the month. Also, five more adult females either left the area or were captured by enemies. Young may have succumbed to the unusually high temperatures in this relatively exposed habitat. The temperature at Lawrence was 8.4 degrees above average. The highest reading of the year (105° F.) was in June. For the state as a whole it was the warmest June on record. Vegetation was harmed and there were many consecutive nights without dew. Precipitation was 3.82 inches less than average. Trap disturbances by predators increased in June and by late July results of trapping were not worth the expenditure of effort. Operations were discontinued on July 12. In August the population was increased by the appearance of two subadults but both disappeared in the same month. Thus, of 28 rats caught in the woodland houses in 1952, only three survived

into 1953, and they left the area. Two were captured for the last time at the western section of outcrop and the third, a female, returned to bear young in 1953. The loss of 89.3 per cent of the population in less than a year is much too great for a rodent with a relatively low reproductive potential to overcome.

In June, 1953, two adults, male and female, and two juveniles were captured, but only the adult female was caught after June. After she disappeared in August all the houses were abandoned and trapping operations were terminated.

Five adult females and five juveniles (two males and three females) were caught at the western section of outcrop in June, 1952, when trapping was begun there. There was no trap disturbance, but by the end of August, four of the adult females and four juveniles had disappeared. In three nights of live-trapping in September only two individuals were living at this part of the outcrop—a previously marked adult female and a subadult female first caught in June as a juvenile. In the summer of 1953, seven woodrats, all new (three adult females and four juveniles), were living at the outcrop. However, in autumn only two individuals remained—an old subadult female and a new subadult female.

Discussion

Factors Affecting Populations

In the area of my study, for at least eight years prior to 1949, the climatic pattern was good for woodrats. According to reports of competent observers, woodrats were numerous in every habitat type especially on wooded hillsides and hilltops in 1947 and early 1948. At present (1955) they are rarely found in these situations. Evidence of decimating losses in March of 1948 and January of 1949 coinciding with extremes of low temperature with ice and snow storms, have been reported in a separate paper (Fitch and Rainey, 1956:506, 507).

Most small-mammal populations rapidly increase after such disasters, but factors which are not readily detectable have prevented an increase in woodrats. The reproductive potential of the woodrat is relatively low and it would take a longer period of time than would a more prolific species to regain peak abundance. If the number of breeding females is depleted, the recovery period is much prolonged. Even under optimum conditions it almost certainly would take more than one year for the rats to repopulate less favorable areas. In 1951, heavy rains at the time young were be-

ginning to disperse and drought in 1952 and 1953 would perhaps retard to a certain extent reinvasion of the depopulated areas. Extensive destruction or disturbance of hedge rows in the area of study, by man, likewise has resulted in deterioration of habitat and has tended to retard spread into less favorable areas which were formerly occupied. When numbers are exceptionally low, especially in species that live in small colonies, important natural enemies perhaps could prevent a rapid build-up. Both sexes tend to roam more when numbers are low and vulnerability to predators would increase. In this area which is near the northeastern limits of the range of the eastern woodrat, optimum habitat is not so abundant as it is nearer the center of the range. When numbers are low, the ability of rats to repopulate their habitat is greatly reduced because of discontinuity of habitat. If a population is reduced or destroyed in suboptimum situations at the center of the range, re-establishment in these situations would take place faster because of proximity of unaffected populations in optimum habitats.

The number of woodrats in a colony in this area is ordinarily stabilized and the welfare of the colony is strongly dependent on the survival or replacement of productive females. In 1952, juveniles were numerous at the woodland houses and western section of outcrop, but they were scarce at the eastern section of outcrop since this section lacked breeding females. For the population to hold its own, young must be produced at a rate at least equal to the rate at which adults disappear. An example of stabilized conditions and the disastrous consequences involved in their alteration was observed in the colony of rats living in the hedge row described earlier (page 566). Five rats were caught in snap traps at five houses on November 11, 1953. All except one of the remaining seven houses had indications of being occupied. Four of the five houses from which rats were caught were completely dismantled in November and December, 1953. When the area was revisited in early 1955, none of the remaining houses was occupied, and all appeared to have been deserted at least since the autumn of 1954. There was no stored food in any of the houses.

Distributional Patterns and Factors Limiting Dispersal of Populations

Wooded stream courses, and rock outcrops either associated with stream courses or away from them seem to provide the chief dispersal routes for woodrats in Kansas. Hedge rows are important in eastern Kansas but are not present in western Kansas. In Cook

County, Texas, Bailey (1905:109) found *osagensis* in wooded ravines and Russell (1953:461) found it inhabiting dense growths of low shrubs along intermittent streams in the same area. In Oklahoma this woodrat is generally associated with rocky bluffs and wooded, rocky ravines and also occurs in the oak-elm flood-plain forests in the eastern part of the state (Blair, 1939:124). McCarley (1952:108) found it common in the postoak-blackjack and flood-plain forest association in Byron County, Oklahoma. In the vicinity of Stillwater, Payne County, Oklahoma, Murphy (1952:205) reported that *osagensis* preferred the postoak-blackjack ravine situations. Black (1936:33) found it along cliffs and in caves of northwestern Arkansas. In south-central Missouri, Moore (1938:503) observed it inhabiting water-worn cavities in limestone bluffs bordering streams. Also in south-central Missouri, Leopold and Hall (1945:145) observed that *osagensis* lived in crevices in a limestone cliff and in uninhabited buildings.

The Osage Cuestas (Schoewe, 1949:282) are prominent physiographical features of eastern Kansas south of the Kansas River. According to Schoewe (*loc. cit.*) the cuestas ". . . consist of a series of northeast-southwest irregularly trending east-facing escarpments between which are flat to gently rolling plains." The tops of these escarpments are capped by a stratum of limestone and when not covered by deposited soil the edge of the stratum is exposed forming an outcrop. Major streams tend to flow transverse to the escarpment and tributaries tend to follow the vales in between. Erosional action of these streams cutting through bedrock produces rocky ledges along the banks which serve as habitat for woodrats. Kellogg (1915:185) in writing of this woodrat in southeastern Kansas reported that it inhabited cliffs and rocky ledges along streams. He further states: "Old settlers in Labette and Cherokee counties informed me that during the seventies, wood rats were plentiful among the rocks and sandstone ledges near streams." Streams in the Flint Hills have cut deep channels lined with outcropping rock ledges. These and the thicket-covered banks provide requirements for woodrat habitat.

In an early report, Knox (1875:21) stated that woodrats (*N. f. campestris*) were common along the streams of middle and western Kansas. Kellogg (1915:183) recorded woodrats in northwestern Kansas as living along chalk and sandstone ledges. Hibbard (1933: 80) reported them from wooded hillsides along tributaries of the Republican River in northwestern Kansas and chalk bluffs along

the Smoky Hill River and its tributaries in western Kansas. Cockrum (1952:188) also states that the western subspecies usually is found along rock ledges. I have seen houses of *campestris* along extensive outcrops of rock in western Kansas and also in juniper trees growing near the outcrops. Information regarding habitat preferences north of Kansas is scanty. Jones (1954:485) records *campestris* as living in dense thickets and uninhabited buildings in southwestern Nebraska. Bailey (1905:109) reported the subspecies, *baileyi,* living in caves and cliffs of the timbered canyons of north-central Nebraska.

The eastern woodrat has never been reported from southeastern Nebraska, although there are specimens in the University of Kansas Museum of Natural History collected one mile west of Vermillion, Marshall County, Kansas, only 19 miles south of the Nebraska border. To determine those environmental factors preventing further northward dispersal, I made several trips into northeastern Kansas and southeastern Nebraska (see Fig. 13).

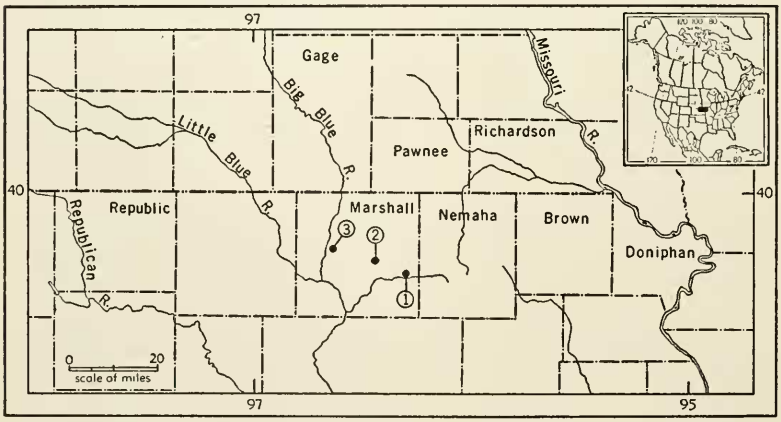


Fig. 13. Counties in northeastern Kansas and southeastern Nebraska investigated for occurrence of the eastern woodrat. Localities of known occurrence, all in Marshall County, are: (1) 1 mi. W Vermillion, (2) 5½ mi. S Beattie, (3) 2 mi. S Marysville.

In the summer of 1954, an intensive search was made for woodrats in Doniphan and Brown counties and in parts of Nemaha County. None was found. In eastern Marshall County, five and one-half miles south of Beattie, numerous houses were found in a large hedge row. The search was extended straight north from this locality into Nebraska. Several residents of Summerfield, Marshall County, Kansas, a small town at the Kansas-Nebraska